

THE CARPOLESTIDAE EARLY TERTIARY PRIMATES FROM NORTH AMERICA

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Dedicated to
the memory of
Professor Glenn Lowell Jepsen
1903-1974

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ABSTRACT. The Carpolestidae were archaic primates of the superfamily Plesiadapoidea. They have been recovered from strata of Middle Paleocene (Torrejonian) to early Eocene (Wasatchian) age in western North America. Although known only from jaws, teeth, and a few cranial fragments, carpolestids have very characteristic dentitions by which they are easily recognized. Most diagnostic are the enlarged, serrate P_4 , and the enlarged, polycusate P^3 and P^4 .

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The systematic revision includes emended diagnoses for all taxa. Three genera, *Elphidotarsius*, *Carpodaptes*, and *Carpolestes*, are recognized. There are nine valid species: two in *Elphidotarsius*, five in *Carpodaptes* (including one new species), and two in *Carpolestes*. *Saxonella*, a Middle Paleocene primate from Europe originally described as a carpolestid, is an aberrant plesiadapoid, here placed in a family separate from carpolestids and plesiadapids.

New material described provides the first published information on the upper teeth of *Elphidotarsius*, the lower incisors of *Elphidotarsius* and *Carpolestes*, the anterior teeth of *Carpolestes*, the posterior part of the mandible of *Carpodaptes*, and the snout of *Carpolestes*, as well as additional evidence bearing on dental formulae and intraspecific variability.

Analysis of wear facets indicates that the molars of carpolestids resemble those of plesiadapids not only morphologically, but also functionally; they were used in the shearing (Phase I) and grinding (Phase II) stages of mastication. The specialized premolars were probably most important during the "puncture-crushing" stage, when the blade-like P_4 was used to tear or cut food. They were less important during Phase I and probably ineffective during Phase II.

The three genera, *Elphidotarsius*, *Carpodaptes*, and *Carpolestes*, form a natural sequence both morphologically and stratigraphically, indicating that they are representatives of a single generic lineage. Each is rather restricted temporally: *Elphidotarsius* has been found only in Torrejonian beds, *Carpodaptes* is known chiefly from Tiffanian strata, and *Carpolestes* occurs in "Clarkforkian" and earliest Wasatchian deposits.

The nature and extent of similarities between

carpolestids and plesiadapids indicates that the two families are closely related through a common ancestor.

INTRODUCTION

The radiation of primates in the Paleocene was one of the most successful episodes in the early evolution of eutherians. In North America, members of this initial deployment, particularly plesiadapids, became common or even dominant forms in many local faunas. Other "archaic prosimians" included in this first major radiation of lower primates were the Paromomyidae (including *Phenacolemur*), the Carpolestidae, and, according to some authors, the Picrodontidae and the Microsyopidae. (Recent attempts [e.g. Cartmill, 1972; Martin, 1968] to banish the "archaic prosimians" from the Primates or to transfer them to the Insectivora are unjustified when available evidence is considered *in toto*.)

Renewed interest has focused on these early primates in recent years, resulting in a few broad reviews (e.g. Simons, 1963, 1972; McKenna, 1966; Szalay, 1968a, 1972b). There have also appeared several more specific works that have contributed significantly to our understanding of Paleocene primates (e.g. Simpson, 1955; D. E. Russell, 1959, 1964; Szalay, 1968b, 1969a, 1969b, 1972a; Gazin, 1971; Butler, 1973; Gingerich, *in press*; and Bown and Gingerich, 1972, 1973). One outcome of the current crescendo of interest in early primates has been the realization of their great diversity, and also of the presence of features in common which unite them more or less closely as members of the Primates. The relationships of these early forms to primates of Eocene or later time have been a subject of investigation. It has long been known that Paleocene *Plesiadapis* and *Phenacolemur* gave rise to Eocene species of the same genera. Recent evidence has strengthened the possibility that some other Paleocene primates may also have had Eocene descendants, e.g. *Plesiolestes* is a

plausible ancestor for some Eocene microsyopids (Bown and Gingerich, 1972, 1973).

The interrelationships of the Paleocene primate families and genera are still not fully understood, but a relatively clear picture of affinities and evolutionary trends can be reconstructed in some cases. One family for which this is now possible, the Carpolestidae, forms the subject of this paper. This aberrant group comprises three genera that have been found in deposits of Middle Paleocene to earliest Eocene age in western North America. The three genera, *Elphidotarsius*, *Carpodaptes*, and *Carpolestes*, constitute a well-documented time-transgressive structural sequence.

The Carpolestidae are known solely from dentitions and gnathic and cranial fragments; unfortunately, no postcranial elements can be confidently referred to the family. Such evidence as has been available has suggested close ties between the Plesiadapidae and the Carpolestidae, but a number of peculiar features clearly segregate the latter at the family level from all other early primates. The most conspicuous feature (and also the most significant taxonomically) is the specialized lower fourth premolar. Through time this tooth became progressively enlarged, multicusped, and bladelike. Concomitant with this development was the reduction of the anterior dentition, except for the large, procumbent medial incisor, which remained prominent in size throughout the lineage. This particular combination of features in the mandibular dentition has evolved independently in several unrelated mammalian groups and has been termed the "plagiolacoid dentition" (Abel, 1931; Simpson, 1933; also see below, p. 51). As hypertrophy of P_4 proceeded in carpolestids, there was corresponding enlargement of the upper third and fourth premolars (which occlude with P_4). P^3 and P^4 lengthened anteroposteriorly and developed three longitudinal crests bearing cuspules, somewhat resembling upper molars in multituberculates. (In fact, the first discovered

upper premolar of a carpolestid was mistaken for a tooth of a multituberculate.) These features have been and still are regarded as diagnostic of the family Carpo-lestidae.

Since the discovery of the first carpolestid specimen about half a century ago, only a small number of articles on carpolestids have appeared, and most have been descriptions of new taxa. By 1970, only about twenty specimens had been described or figured in the literature, but large numbers of specimens had been recovered which remained unpublished. Persistent field work in Paleocene deposits has produced sizable samples of these specialized early primates (the largest single species sample from one site is greater than 60 specimens). More than 300 specimens are now known, many of which reveal information previously unknown. The most extensive collections have been recovered for Princeton University by field operations under the direction of Professor G. L. Jepsen; these investigations have been undertaken in the Bighorn Basin for more than forty years. Only three carpolestid specimens discovered by the earliest of these expeditions have been described previously (Jepsen, 1930). The extensive Princeton collection, as well as numerous other new specimens, provide ample carpolestid material to serve as the basis for a systematic revision. In addition, better preserved specimens and samples of larger size can now contribute significantly to our understanding of carpolestids and their role in the initial radiation of the Primates.

ABBREVIATIONS

AMNH	— American Museum of Natural History, New York
CM	— Carnegie Museum, Pittsburgh
MCZ	— Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
PU	— Princeton University Museum, Princeton, New Jersey

ROM	— Royal Ontario Museum, Toronto, Ontario
UA	— University of Alberta, Edmonton
UKMNH	— University of Kansas Museum of Natural History, Lawrence
UMMP	— University of Michigan Museum of Paleontology, Ann Arbor
UMVP	— University of Minnesota, Minneapolis
USNM	— United States National Museum, Washington, D.C.
UW	— University of Wyoming, Laramie
YPM	— Peabody Museum of Natural History, Yale University, New Haven, Connecticut
B	— Breadth
L	— Length
MD	— Mandibular depth, measured on the buccal side beneath the anterior root of M_1 .
N	— Number of observations (specimens)
OR	— Observed range
s	— Standard deviation
V	— Coefficient of variation
\bar{X}	— Mean

Dental terminology used in this study is that of Szalay (1969a). Dimensions of the cheek teeth and depth of the mandible have been measured in the manner illustrated in Figure 1, using an ocular micrometer fitted to a lens of a binocular microscope.

HISTORY OF STUDY

The first carpolestid described was *Carpodaptes aulacodon* Matthew and Granger (1921). The generic name means "fruit eater"; the specific name alludes to the vertical grooves on the lower fourth premolar, a condition similar to that of P_4 in plagiaulacoid multituberculates and certain marsupials. The species was based solely on the type specimen and, in the absence of any comparable species, Matthew and Granger were duly reluctant to suggest its

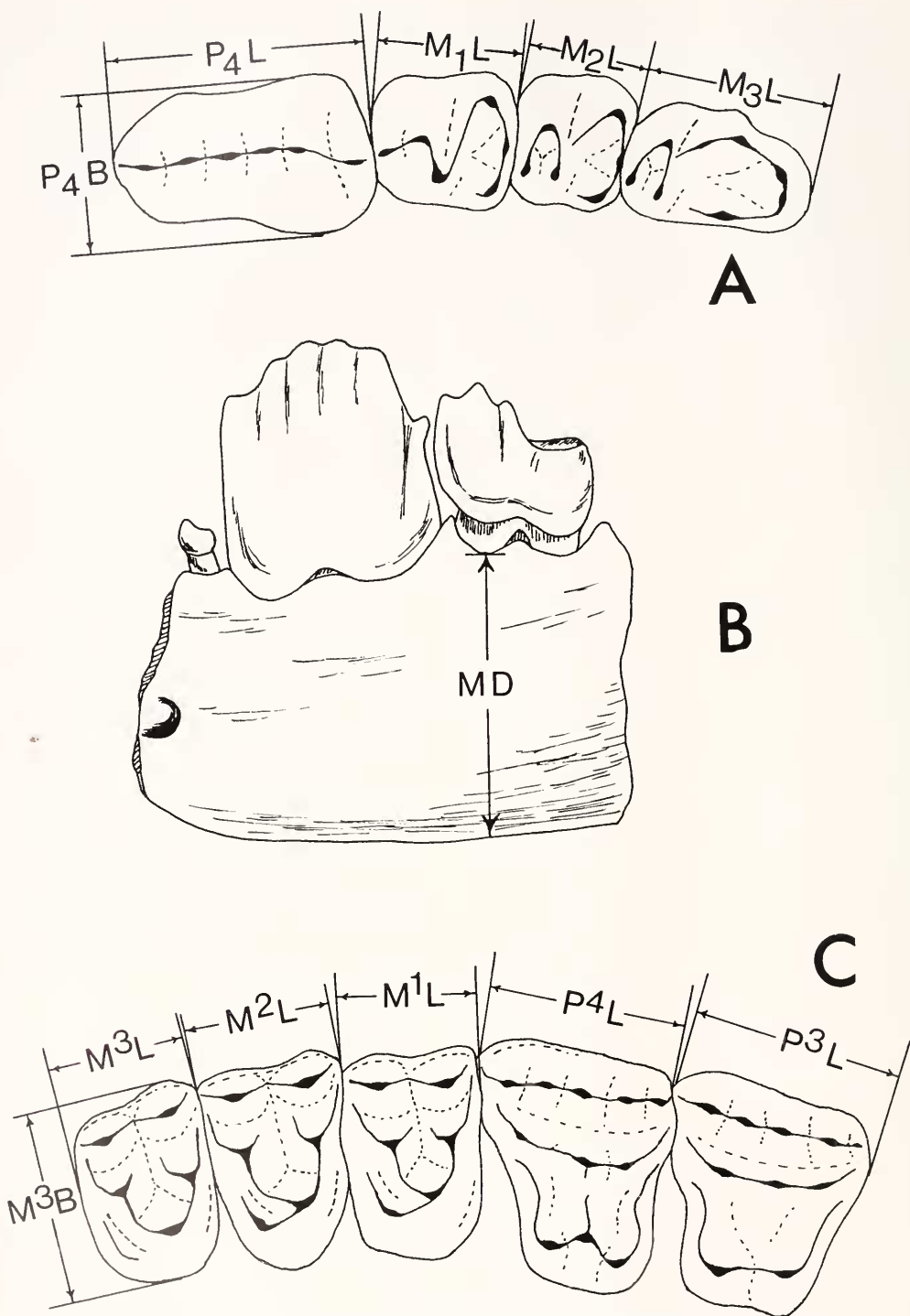


Figure 1. Schematic drawings to demonstrate method of taking measurements. All dimensions are in millimeters. A) crown view of P_4 - M_3 . L = maximum mesiodistal length, as shown. Breadths (B) are maximum dimensions measured perpendicular to length. B) lateral view of mandible. MD = mandibular depth beneath anterior root of M_1 . C) crown view of P^3 - M^3 .

affinities. They speculated only that "it may be a primate, a menotyphlan insectivore, or neither" (Matthew and Granger, 1921:6).

J. W. Gidley (1923) proposed *Elphidotarsius florenceae* for a mandibular fragment preserving P_4 through M_3 . Again the holotype was the only known specimen. He noted resemblances of the molars to those of fossil tarsoids such as *Tetonius*, therefore placing *Elphidotarsius* provisionally in the Tarsiidae, the name then applied to many Paleocene and Eocene primates. He did not compare the specimen to *Carpodaptes*.

Carpolestes ("fruit stealer") was named by Simpson (1928) to accommodate the new species *Carpolestes nigridentis* from the Eagle Coal Mine at Bear Creek, Montana. Simpson regarded *Carpolestes* as a close relative of *Carpodaptes*, classifying both as aberrant members of the Tarsiidae. The following year he described a second species from Bear Creek, *Carpolestes aquilae* (Simpson, 1929).

Jepsen (1930) named a third species of *Carpolestes*, *C. dubius*. Included in his hypodigm was a maxilla with four teeth, the first upper dentition of a carpolesiid to be identified. Jepsen recognized that the type and only known specimen of the supposed multituberculate *Litotherium complicatum* (Simpson, 1929), an isolated upper premolar from Bear Creek, was actually P^3 of *Carpolestes*. (This eliminated the Multituberculata from the known fauna of Bear Creek.) Like Matthew and Granger, he deferred definite ordinal assignment for *Carpolestes*, stating, "It is possible to select suites of characters which, taken by themselves, would place *Carpolestes* in any one of several orders," (Jepsen, 1930:523).

The relationship of *Elphidotarsius* to *Carpodaptes* and *Carpolestes* was recognized by Simpson (1935b), who proposed the family Carpolestidae for the reception of the three genera. He also noted adaptive features shared by this family, the Plesiadapidae, and the Apatemyidae. As diagnostic characters of the Carpolestidae,

Simpson listed the enlarged lower fourth premolar and the procumbent enlarged lower incisor. The dental formula remained controversial, however. Jepsen (1930) had proposed the mandibular dental formula 1.0.4.3, regarding the tooth immediately behind the enlarged incisor as P_1 . Simpson (1935b:10), although conceding that it was "impossible to determine whether the following tooth is a canine or P_1 ", considered it "slightly more probable that it is the canine". Discussing the degree of relationship among the three genera, Simpson (1937b:161) remarked that the morphologic sequence *Elphidotarsius-Carpodaptes-Carpolestes* "may be a direct phylogeny, although the possible age difference between the last two genera seems too small to permit such a marked structural advance in a direct descendant, and it is more likely that some collateral evolution is involved".

In 1936, Simpson described *Carpodaptes hazelae* from the Scarritt Quarry in the Crazy Mountain Field of Montana. The next year, he described the most complete known upper dentition of a carpolesiid (referable also to *C. hazelae*), preserving three molars and four antemolar teeth. The most anterior tooth unfortunately has been lost since Simpson's description, and it is not preserved in any carpolesiid found subsequently. In the same paper, Simpson (1937a) reasserted his view that carpolesiids represent early aberrant primates and again stressed the resemblances to *Plesiadapis*, concluding that these similarities could only indicate close affinity and common ancestry.

Dorr's field work in the Hoback Basin of western Wyoming yielded a Tiffanian fauna which included a previously unknown carpolesiid, *Carpodaptes hobackensis* (Dorr, 1952). Dorr suggested that this species might be more nearly intermediate between *Elphidotarsius* and *Carpolestes* than either other named species of *Carpodaptes*.

Gazin (1956b) reported the occurrence of *Carpolestes*, cf. *C. dubius*, in latest Paleo-

cene beds near Buckman Hollow, southwestern Wyoming, the only record of a carpolestid in the southern part of the Green River Basin.

The Carpolestidae were regarded as strictly North American until the description of *Saxonella*, from Walbeck, Germany, by D. E. Russell (1964). Due to several significant differences between the North American carpolestids and the new European form, Russell was obliged to redefine the family in order to include *Saxonella*, and to create two subfamilies, the Carpolestinae (for the three North American genera) and the Saxonellinae (for *Saxonella*). This classification was adopted by some subsequent authors (e.g. Romer, 1966; McKenna, 1967). Nevertheless, *Saxonella* seems to have as much or more in common with plesiadapids. Some similarities were mentioned by Russell (1964). Szalay (1968a, 1969a) reiterated the resemblances and intimated a relationship between *Saxonella* and the Plesiadapidae. Van Valen (1969) went a step further and formally placed the Saxonellinae in the Plesiadapidae. He grouped Carpolestidae with the Paromomyidae, Microsyopidae, Plesiadapidae, and Picrodontidae in a new superfamily, the Microsyopoidea.

The first carpolestids from the Paleocene of Canada were reported by L. S. Russell (1967). He referred three fragmentary specimens from Alberta to a new species, *Carpolestes cygneus*. As noted by Kristalka (1973), however, this species is clearly referable to *Carpodaptes*. Kristalka described additional specimens of *Carpodaptes* from Canada, this time from the Cypress Hills of southeastern Alberta.

Both *Carpodaptes* and a new species of *Elphidotarsius*, *E. shotgunensis*, were recorded in the Shotgun Local Fauna of western Wyoming (Gazin, 1971). The association of two different genera of carpolestids is otherwise unknown.

Szalay (1972b) suggested that the genus *Carpolestes* should probably be regarded as a synonym of *Carpodaptes* (a view

depicted in a chart by Szalay earlier [1969a: fig. 27], but not mentioned in the text of that paper). He also proposed a new interpretation of the dental formulae of carpolestids. In analogy with his interpretation of the formula in *Pronothodectes* and in Middle Paleocene paromomyids, he sug-

gested the formula $\frac{2.1.3.3}{2.1.3.3}$ or *Elphido-*

tarsius, and the same formula, except for the loss of P_2 , for *Carpodaptes* and *Carpolestes*. He also figured a tooth as the first known upper incisor of a carpolestid (Szalay, 1972b: fig. 1-9).

Other notable discussions of the Carpolestidae not cited above include those of Abel (1931), Simpson (1940), Hill (1953), Saban (1961), and Simons (1963, 1972).

STRATIGRAPHIC AND GEOGRAPHIC OCCURRENCE

Carpolestids have been discovered in beds of Middle Paleocene (Torrejonian) to earliest Eocene (Wasatchian) age in the Rocky Mountain region of western North America (see Fig. 2). Where different genera have been found in the same depositional basin, they occur in stratigraphic succession, *Elphidotarsius* below *Carpodaptes* (except in the Shotgun Local Fauna), and *Carpodaptes* below *Carpolestes*. The temporal range of each genus appears to be rather strictly limited, suggesting that carpolestids may be of value in determining the approximate ages of faunas. *Elphidotarsius* is known only in beds of Torrejonian age. Its latest known occurrence is in the late Torrejonian Shotgun Local Fauna, where it is associated with the earliest known *Carpodaptes*. All other records of *Carpodaptes* are restricted to the Tiffanian (Late Paleocene). *Carpolestes* first appears in the Silver Coulee beds of the northern Bighorn Basin (Princeton Quarry level) and is known from several sites regarded as "Clarkforkian" (latest Paleocene) in age, as well as a few of Early Eocene age.

Only at Shotgun do two carpolestid species occur together. The Shotgun Local Fauna is diverse, and the sample is very large but consists predominantly of isolated teeth. Included in the fauna are other pairs of related genera rarely or never found together elsewhere. There has been some question as to the age of the Shotgun fauna and, in fact, whether the entire assemblage is the same age. Some forms suggest a late Torrejonian age while others are more indicative of the Tiffanian. Patterson and McGrew (1962) believed that the fauna indicated an early Tiffanian age, but more recently they (personal communication, 1973) and C. B. Wood (personal communication) regard the age as late Torrejonian.

The primates, described by Gazin (1971), include *Palaeacchthon*, *Palenochtha*, *Plesiolestes*, *Paromomys*, and *Elphidotarsius* (all recorded only from Torrejonian deposits), *Pronothodectes* (usually from the Torrejonian but known also from the early Tiffanian [Gazin, 1956a]), and *Phenacolemur*, *Plesiadapis*, and *Carpodaptes* (all typically Tiffanian or later in age). From the progressive nature of some species of the Torrejonian genera, Gazin (1971) inferred a late Torrejonian age for the Shotgun assemblage (as he had earlier, [Gazin, 1961]), but he conceded that the presence of the three genera otherwise unknown in pre-Tiffanian faunas¹ "might suggest a mixture of materials from different levels" (Gazin, 1971:15).

The latter hypothesis is more compatible with the primate evidence, particularly the carpolestids. Specimens of *Carpodaptes* from Shotgun bear closest resemblance to those from Cedar Point Quarry (definitely of Tiffanian age) and, as noted above, *Carpodaptes* has not been found at any

other pre-Tiffanian site. But aside from the primates, the fauna is overwhelmingly Torrejonian in aspect, with few Tiffanian forms; the reverse would be expected in a Tiffanian deposit containing reworked Torrejonian fossils. Resolution of this problem is, however, beyond the scope of this paper, and herein the age of the Shotgun Local Fauna is accepted as late Torrejonian.

The uniqueness of the Shotgun fauna may be due in part to its unusual paleo-environment. In late Paleocene time, the site was flanked on the east by the extensive, probably saline Waltman Lake, which was connected at least intermittently to the Cannonball Sea (McGrew, 1963). Similar paleoecological conditions have not been sampled elsewhere in the North American Paleocene.

Mention should also be made of the "Clarkforkian" problem. The use of this term, proposed by H. E. Wood, et al., (1941), has met some opposition in recent years. For example, R. C. Wood (1967), who reviewed the Clark Fork fauna and stratigraphy, concluded that available evidence "scarcely warrants recognition of the Clark Fork as a provincial age, faunal zone, or member of the Polecat Bench Formation" (Wood, 1967:28). Nevertheless, field work in the type Clark Fork area and in other Late Paleocene deposits in recent years has yielded considerable new evidence suggesting that the term "Clarkforkian" may be valid and useful as a North American Land Mammal "Age" (D. C. Parris, R. E. Sloan, personal communication). The genus *Carpolestes* has been regarded as characteristic of the "Clarkforkian" (Sloan, 1969: fig. 5) and is one of several forms whose overlapping temporal ranges may be used in a redefinition of the "Clarkforkian" (Sloan, *in litt.*, 5/22/73). Sloan (1969) placed Princeton Quarry just below the Tiffanian-"Clarkforkian" boundary; more recently he suggests that it is approximately at the boundary (Sloan, personal communication, 6/28/73). He regarded Olive, Bear

¹The only purported Torrejonian record of *Plesiadapis* is in the Battle Mountain Local Fauna of the Hoback Basin, first considered of Torrejonian age (Dorr, 1958), but now regarded as early Tiffanian (Gingerich, personal communication).



Creek, and Buckman Hollow to be within the "Clarkforkian" (Sloan, 1969). Except for the Olive Local Fauna, here considered Tiffanian, I have adopted Sloan's view and regard the Princeton Quarry level as earliest "Clarkforkian". Pending a revised definition

of the "age" (Sloan and Parris, in preparation), the name "Clarkforkian" appears herein in quotation marks.

To date, more than 300 carpoilestid specimens (mostly jaws) have been collected (*Elphidotarsius*: 30+; *Carpodaptes*: 200+;

Carpolestes: 80+). They are among the commonest mammals at many Middle and Late Paleocene sites, and one may infer that they were not uncommon members of the bioocenose. For example, in the Polecat

Bench sequence, more than 20 jaws of *Elphidotarsius* are included in the collection from Rock Bench Quarry, and more than 60 jaws of *Carpodaptes* have been recovered at Cedar Point Quarry, making it

←

Figure 2. Map of localities where carpolestids have been found.

Locality	Age	Formation	Occurrence	Reference to locality or to carpolestid record
1) Swan Hills	Late Paleocene (Tiffanian)	Paskapoo	<i>Carpodaptes cygneus</i>	L. S. Russell, 1967
2) Cypress Hills	Late Paleocene (Tiffanian)	Ravenscrag	<i>Carpodaptes</i> , cf. <i>C. cygneus</i>	Krishtalka, 1973
3) near Roche Percee	Late Paleocene (Tiffanian)	Ravenscrag	<i>Carpodaptes cygneus</i>	Krause, personal communication
4) Crazy Mountain Field				
a) Gidley Quarry	Middle Paleocene (Torrejonian)	Fort Union (Lebo Member)	<i>Elphidotarsius florencae</i>	Gidley, 1923; Simpson, 1937b
b) Scarritt Quarry	Late Paleocene (Tiffanian)	Fort Union (Melville Member)	<i>Carpodaptes hazelae</i>	Simpson, 1936
c) Princeton Loc. 11	Late Paleocene (Tiffanian)	Fort Union	<i>Carpodaptes</i> sp.	Simpson, 1937b
5) Eagle Coal Mine at Bear Creek	Late Paleocene ("Clarkforkian")	Fort Union	<i>Carpolestes nigridens</i>	Simpson, 1928, 1929
6) Circle	Late Paleocene (Tiffanian)	Tongue River	<i>Carpodaptes</i> , cf. <i>C. hazelae</i>	Sloan, in D. E. Russell, 1967
7) Olive	Late Paleocene (Tiffanian)	Tongue River	<i>Carpodaptes</i> sp.	Sloan, in D. E. Russell, 1967
8) Medicine Rocks Site 1 near Ekalaka	Middle Paleocene (Torrejonian)	Tongue River	<i>Elphidotarsius</i> , cf. <i>E. florencae</i>	Princeton University site, unpublished
9) Judson	Late Paleocene (Tiffanian)	Tongue River	<i>Carpodaptes</i> , poss. <i>C. cygneus</i>	Holtzman and Sloan, personal communication
10) Polecat Bench region				Princeton University sites, in Jepsen, 1930, or unpublished
a) Rock Bench Quarry	Middle Paleocene (Torrejonian)	Polecat Bench	<i>Elphidotarsius</i> , cf. <i>E. florencae</i>	
b) Long Draw Quarry (Carbon Co., Montana)	Late Paleocene (latest Tiffanian)	Polecat Bench	<i>Carpodaptes jepseni</i> ?	
c) Silver Coulee beds: Princeton, Schaft, Fritz, and Storm Quarries	Late Paleocene (Tiffanian-"Clarkforkian" boundary)	Polecat Bench	<i>Carpolestes dubius</i>	
d) Paint Creek	Paleocene-Eocene boundary	Willwood	<i>Carpolestes nigridens</i>	
e) Twisty-turn Hollow	earliest Eocene (Wasatchian)	Willwood	<i>Carpolestes</i> sp.	
11) Big Horn County				Princeton University sites
a) Cedar Point Quarry	Late Paleocene (Tiffanian)	Polecat Bench	<i>Carpodaptes hazelae</i>	
b) Divide Quarry	Late Paleocene (latest Tiffanian)	Polecat Bench	<i>Carpodaptes jepseni</i>	
c) Cleopatra Reservoir site	Late Paleocene ("Clarkforkian")	Polecat Bench	<i>Carpolestes</i> sp.	
12) Togwotee Pass	Late Paleocene ("Clarkforkian" or Paleocene-Eocene boundary)	"lower variegated sequence"	<i>Carpolestes</i> sp.	McKenna, 1972
13) Dell Creek	Late Paleocene (Tiffanian)	Hoback	<i>Carpodaptes hobackensis</i>	Dorr, 1952
14) Shotgun	Middle Paleocene (latest Torrejonian)	Fort Union (Shotgun Member)	<i>Elphidotarsius shotgunensis</i> and <i>Carpodaptes</i> , cf. <i>C. hazelae</i>	Gazin, 1971
15) Badwater, "Malcolm's Locality"	Late Paleocene (Tiffanian)	Fort Union (Shotgun Member)	<i>Carpodaptes</i> sp.	Krishtalka, personal communication; Black and Dawson, 1966
16) Buckman Hollow	Late Paleocene ("Clarkforkian")	Wasatch (Chappo Member)	<i>Carpolestes</i> sp.	Gazin, 1956b
17) Mason Pocket at Tiffany	Late Paleocene (Tiffanian)	Tiffany	<i>Carpodaptes aulacodon</i>	Matthew and Granger, 1921; Simpson, 1935b

second in abundance to *Plesiadapis* at this productive site. On the other hand, carpo-lestids are decidedly less common at some localities, such as the Crazy Mountain Field, where only 11 specimens of *Carpodaptes* are known from Scarritt Quarry, and only a single jaw of *Elphidotarsius* has been recorded among 382 identifiable mammalian jaws from Gidley Quarry (Simpson, 1937b:34). Nevertheless, the wide geographic distribution and often common occurrence of carpoolestids contribute to their utility in correlating Paleocene faunas.

SYSTEMATIC REVISION

Maglio (1971:372) recently stated:

"... the goal of the paleo-biologist ... is not the recognition of fossil "taxa" and the establishment of a formal terminology for ever smaller segments of a phyletic continuum. On the contrary, it is the establishment of evolutionary units that can be traced through long periods of time and with which broad evolutionary phenomena can be studied."

I concur with this view. Systematics should be a means for better understanding animals and their evolution; it should not be an end in itself. The systematic revision presented here has been approached with this in mind. Synonymy of named species has been proposed only when there can be little doubt that the taxa involved are conspecific. Closely similar established species have been retained when any consistent distinctions could be discerned. New species have not been proposed unless specimens were demonstrably different from existing species. I believe that this somewhat conservative approach will promote a clearer understanding of the evolution and interrelationships of the Carpoolestidae.

Order **PRIMATES** Linnaeus, 1758

Infraorder **PLESIADAPIFORMES**
Simons, 1972¹

Superfamily **PLESIADAPOIDEA**
Trouessart, 1897

Family **CARPOLESTIDAE** Simpson, 1935

Carpoolestidae Simpson, 1935b: 9.

Type Genus: *Carpolestes* Simpson, 1928.

Included Genera: *Carpodaptes*, *Elphidotarsius*, and *Carpolestes*.

Distribution: Middle Paleocene (Torrejonian) to Early Eocene (early Wasatchian) of western North America (Alberta, Saskatchewan, Montana, North Dakota, Wyoming, and Colorado).

Emended diagnosis: Very small aberrant

primates. Dental formula $\frac{P2.P1.P3.3}{2.1.2-3.3}$. Man-

dibular dentition characterized by enlarged, rooted, anteriorly inclined medial incisor, followed by greatly reduced tooth (lateral incisor). Root of enlarged incisor implanted at about 45° angle to vertical and extending back no further than to a point beneath P₃. Canine present but also much reduced. P₁ absent; P₂ either very small and button-like (*Elphidotarsius*) or lost (*Carpodaptes* and *Carpolestes*). P₃ small, double-rooted (*Elphidotarsius*), or single-rooted (*Carpodaptes* and *Carpolestes*). P₄ enlarged (relatively more so in later forms), specialized into polycusate, trenchant blade; talonid heel small, consisting of one cusp, distinct in *Elphidotarsius* and *Carpodaptes*, becoming merged with blade in *Carpolestes*. Proliferation of apical cusps on P₄ occurring in later forms. Molars, except M₁, deviating little from generalized plesiadapid pattern. Trigonid of M₁ longer anteroposteriorly than in M₂ or M₃; widely splayed in *Carpodaptes* and *Carpolestes*, with paraconid directly anterior to protoconid, forming continuation of P₄ blade. Metaconid of M₁ always posterolingual to

¹ This name first appeared in Simons (1972) but was credited to "Simons and Tattersall, 1972", a work which has not been published.

protoconid. Molar talonids broad, basined, with distinct hypoconid and entoconid, small or indistinct hypoconulid (except on M_3). Talonid of M_1 smaller, more compressed anteroposteriorly than in M_2 . M_3 not reduced, with pronounced third lobe bearing two cusps (twinned hypoconulid). P_4 (particularly) and molars exodaenodont. Mandible shallowest in *Elphidotarsius*, deepest in *Carpolestes*.

At least 2 incisors and small canine (?) present in upper jaw. P^2 small, single-rooted, bearing one main cusp. P^{3-4} either of plesiadapid type, smaller than molars, relatively unspecialized (*Elphidotarsius*), or greatly modified, larger than molars, polycusate with 3 longitudinal rows of cusps (*Carpodaptes* and *Carpolestes*). Upper molars with primitive plesiadapid morphology; hypocone small but distinct on M^{1-2} , less distinct or represented by shelf on M^3 .

Discussion: The Carpolestidae were a rapidly evolving group of archaic primates in which extreme specializations of P_4 and P^{3-4} were achieved. The three known genera constitute a sequence that, in general, shows enlargement and specialization through time; they are almost surely in a single lineage. The earliest genus, *Elphidotarsius*, is relatively unspecialized and easily derivable from a form morphologically close to the earliest plesiadapids; it contrasts with *Carpolestes*, in which the family traits are fully manifested.

Teeth in which the base of the crown extends laterally well beyond the roots have been described as "exodaenodont". The condition was first observed in dimylid insectivores (Hürzeler, 1944; Saban, 1958) and later noted in picrodontids and some bats (McGrew and Patterson, 1962). It is especially conspicuous in the lower cheek teeth, particularly P_4 , of carpolestids. Both Hürzeler and Saban suggested that it correlates with malacophagy, but this seems to have little basis. A molluscan diet is very unlikely for picrodontids and bats (as pointed out by McGrew and Patterson,

1962:6), and equally improbable for carpolestids.

The dental formula in carpolestids has been controversial. The interpretation I present differs from that of most previous authors (e.g., Matthew and Granger, 1921; Jepsen, 1930; Simpson, 1935b, 1937b; Dorr, 1952; Hill, 1953; Saban, 1961; and Simons, 1972) and is in accord with that recently proposed by Szalay (1972b). (Justification of the new formula is presented below.)

The upper dental formula is necessarily uncertain, since anterior teeth are known only in the most advanced form, *Carpolestes*, and even in that genus only roots are preserved. If the antemolar teeth are correctly interpreted, there were two incisors, a canine, and three premolars.

Elphidotarsius Gidley, 1923

Elphidotarsius Gidley, 1923: 10; Simpson, 1937b: 162.

Type Species: *Elphidotarsius florencae* Gidley, 1923.

Included Species: *E. florencae* and *E. shotgumensis*.

Distribution: Middle Paleocene (Torrejonian) of Wyoming and Montana.

Emended Diagnosis: Small, relatively unspecialized carpolestids. Lower dental formula 2.1.3.3. Medial incisor (I_1 ?) enlarged and procumbent; crown lanceolate in outline; root extending back to a point approximately below canine. Lateral incisor (I_2 ?) and canine known only from alveoli. Alveolus of P_2 very small, smaller than those of I_2 and P_3 , and situated slightly lingual to them. P_3 premolariform, larger relatively and absolutely than in *Carpodaptes* and *Carpolestes*; crown with prominent apical cusp preceded by lower, less distinct cuspule, and followed by low but distinct heel; two roots, partially fused, occupying a single alveolus. P_4 enlarged (larger than M_1), blade-like, bearing 4 longitudinally arranged apical cusps followed by lower but well defined talonid cusp. M_1

with anteroposteriorly extended trigonid, paraconid and metaconid lingual to protoconid, the metaconid the more lingual of the two. Talonid of M_1 with distinct hypoconid and entoconid. Trigonids of M_2 and M_3 anteroposteriorly compressed. Upper dentition anterior to P^3 unknown. P^3 - M^3 all broader (buccolingually) than long. P^3 distinctly smaller than P^4 , with prominent lingual cusp and major buccal cusp, the latter followed by a smaller buccal cusp. P^4 about same size as M^4 , more triangular, longer buccally, shorter lingually; moderately specialized with buccal row of 4 cusps, median anteroposterior crest bearing large central cusp, and pronounced lingual cusp directly internal to the latter; incipient hypocone at internal end of posterolingual cingulum. Hypocone of molars formed as in P^4 , small, but more distinct than in P^4 , connected to protocone by "nannopithec fold". Pronounced ectocingulum and anterolingual and posterolingual cingula on M^1 - M^3 , weaker on P^3 - P^4 ; cingula not continuous onto lingual face of teeth.

Elphidotarsius florencae Gidley, 1923
Figures 3, 4

Elphidotarsius florencae Gidley, 1923: 10; Simpson, 1937b: 163.

Holotype: USNM 9411, left mandible with P_4 - M_3 .

Hypodigm: type specimen only.

Horizon and Locality: Middle Paleocene (Torrejonian), Lebo Member, Fort Union Formation: Gidley Quarry, Crazy Mountain Field, Montana.

Emended Diagnosis: Less progressive and slightly smaller than *E. shotgunensis*. P_4 and M_1 shorter anteroposteriorly but broader buccolingually than in *E. shotgunensis*. Lower molars as long as, or longer than, broad. Trigonid of M_1 more anteroposteriorly extended (i.e., paraconid and metaconid more widely separated) than in M_2 or M_3 , but less so than in *E. shotgunensis*.

Discussion: Simpson's (1937b) thorough

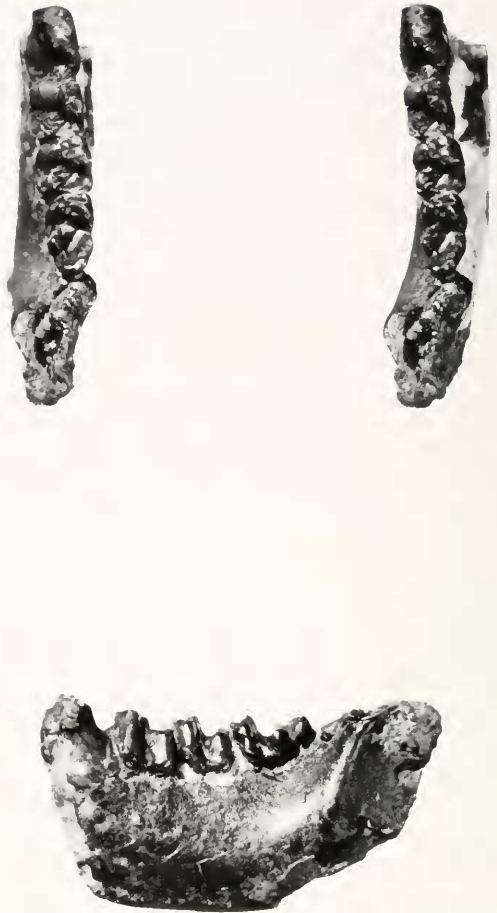


Figure 3. *Elphidotarsius florencae* Gidley, holotype, USNM 9411, left P_4 - M_3 . Crown view (above) and lateral view (below). $\times 6$.

discussion precludes the need for redescription of the holotype. The recently described species *E. shotgunensis* (Gazin, 1971), permits a more precise definition of *E. florencae*. Unfortunately, since only one specimen is known, information on intra-specific variability is unavailable, unless the sample described below, *Elphidotarsius* sp., cf. *E. florencae*, is definitely referable to it.

Elphidotarsius sp., cf. *E. florencae* Gidley
Figures 4B, 5A, 6-8, 34A, 34B

The largest sample of a population of *Elphidotarsius* is from the Middle Paleo-

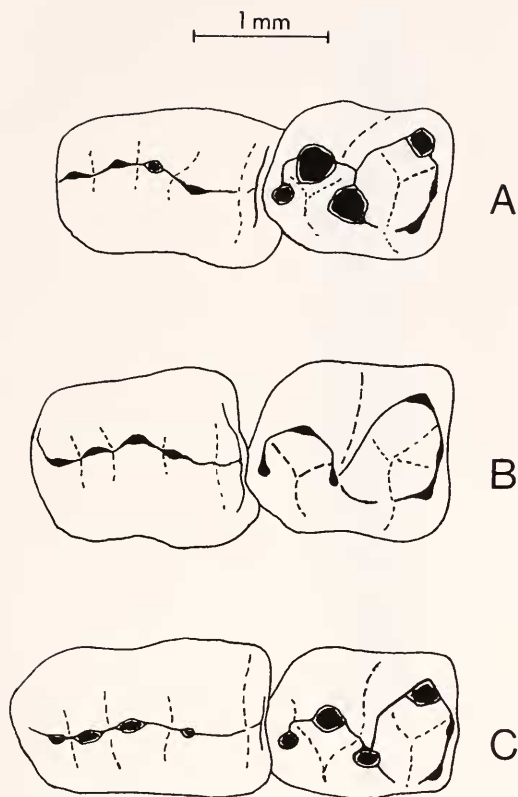


Figure 4. Crown view of right P_4 - M_1 of *Elphidotarsius*, to same scale. A) *E. florencae*, holotype, USNM 9411, from Gidley Quarry. B) *E.*, cf. *E. florencae*, PU 14792, from Rock Bench Quarry. C) *E. shotgunensis*, holotype, AMNH 88311.

cene (Torrejonian) Rock Bench Quarry, Polecat Bench Formation of Park County, Wyoming. The more than twenty specimens are closely comparable to the holotype of *E. florencae*. There are no significant morphologic differences, but the individuals in the Rock Bench sample are, in general, slightly larger than the holotype. A Student's t-test comparing the dimensions of the type with those of the Rock Bench specimens yielded inconclusive results, neither favoring erection of a new species nor declaring the two samples positively conspecific.

Description: The Rock Bench Quarry sample includes many specimens that pro-

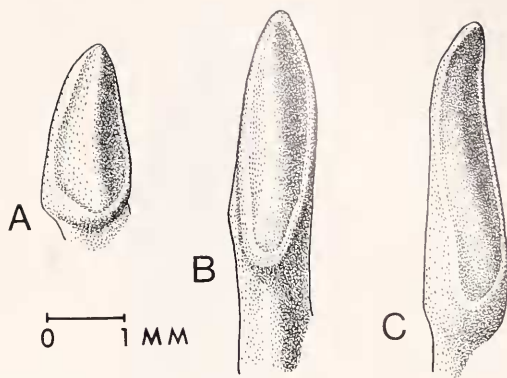


Figure 5. Lower left medial incisors of carpoolestids. A) *Elphidotarsius*, cf. *E. florencae*, PU 14282. B) ?*Carpodaptes* sp., UW 6530 (reversed). C) *Carpoolestes dubius*, PU 14235.

vide new information about *Elphidotarsius*. A few reveal the anterior part of the mandible and suggest the dental formula 2.1.3.3. The Torrejonian plesiadapid *Pronothodectes*, which is close to *Elphidotarsius* in many features (see below), has a similar dental pattern and the formula 2.1.3.3. (e.g., PU 14783; Szalay, 1972b; Gingerich, personal communication). Analogy with *Pronothodectes* strengthens the interpretation of the lower dental formula of *Elphidotarsius* adopted here.

The enlarged medial incisor is preserved in one specimen, PU 14282 (Figs. 5A and 6). It is lanceolate in outline and quite broad at the base, much broader than in either of the other carpoolestid genera. The dorsal (lingual) surface is broad and slightly convex, bounded laterally by a ridge running from the tip to the base of the crown, where it merges with a prominent internal cingulum. The incisor, although shorter, somewhat resembles that of *Plesiolestes*. A small basal cusp arising from the internal cingulum is found in *Pronothodectes* and *Plesiadapis*, but is conspicuously absent from the incisor of *Elphidotarsius*. An interstitial facet is present in PU 14282, but there is no occlusal facet such as observed in *Plesiadapis* by Gingerich (in press).

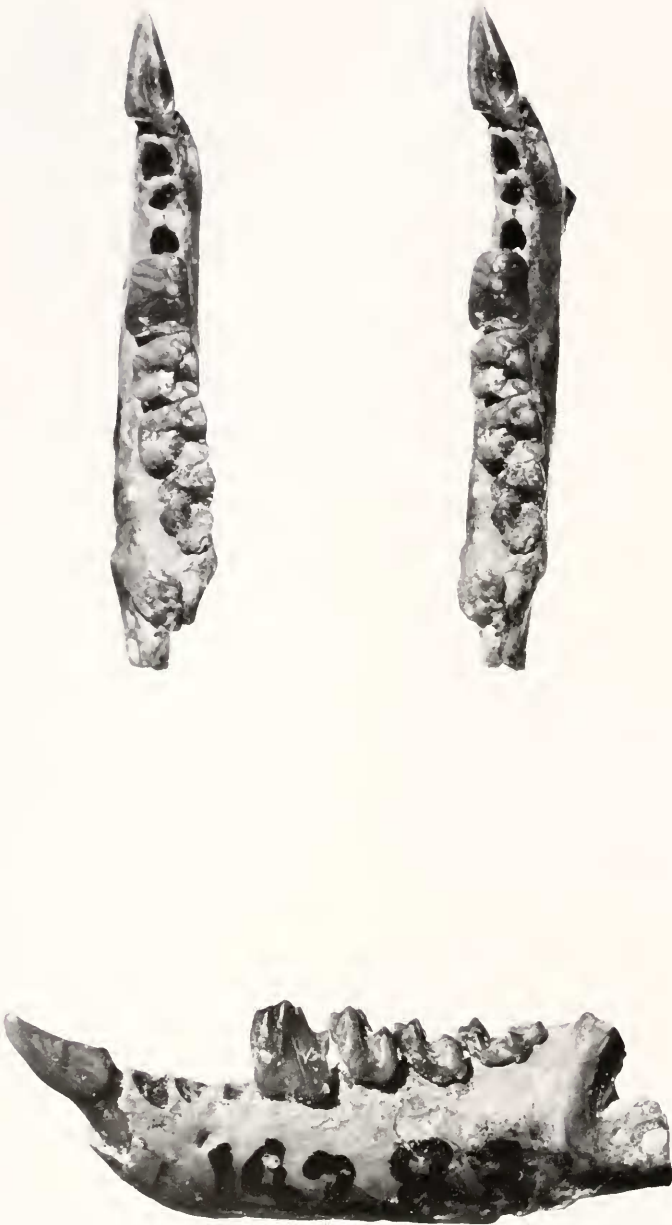


Figure 6. *Elphidotarsius*, cf. *E. florencae* Gidley, PU 14282, left dentary with medial incisor, P_4 - M_3 . Crown view (above) and lateral view (below). $\times 6$. Rock Bench Quarry.

Three alveoli are present between the enlarged incisor and P_3 . They are interpreted to have held I_2 , C, and P_2 . The alveolus just behind the medial incisor is mesiodistally compressed and slightly larger than that for the canine. Its slight anterior inclination suggests that I_2 was somewhat procumbent. The second alveolus is slightly



Figure 7. *Elphidotarsius*, cf. *E. florencae* Gidley, PU 14791, right dentary with P_3 – M_3 . Crown view (above) and lateral view (below). $\times 6$. Rock Bench Quarry.

larger than that of P_2 , supporting the view that it held the canine. The socket for P_2 is situated just lingual to those of the canine and P_3 . Its diminutive size favors the sup-

position that P_2 has been lost in *Carpodaptes* and *Carpolestes*, both of which have one less tooth in the mandible.

P_3 in the Rock Bench sample is pre-

molariform and relatively unreduced. Its two roots are partially joined, occupying a single alveolus. The crown bears a well developed central cusp followed by a low, well differentiated talonid cusp. A short anterior shelf rises in a tiny, low cusp, anterior to the main cusp.

P₄ and the lower molars are very similar to those in the type of *E. florencae*. In some individuals, the cheek teeth (P₄-M₃) are relatively broader buccolingually than in the type. M₂, particularly, is almost always as broad as it is long (as in the type), and often is broader than long. Nevertheless, the extent of variation observed in the Rock Bench sample and in other large samples of carpolestids indicates that this feature is not of taxonomic importance.

P₄ in the Rock Bench sample bears four apical cusps and a lower, pronounced talonid cusp, but it is comparable in length to *E. florencae* and shorter than in *E. shotgunensis*. The third apical cusp is the largest and highest and is probably homologous with the protoconid. (This cusp in the type of *E. florencae* shows apical wear, thus appearing lower than the cusp anterior to it.) Just behind, lower, and slightly lingual to the third cusp is a cusp probably homologous with the metaconid. The second cusp appears to be the homologue of the paraconid and is nearly as prominent as the protoconid. Anterior to it is an accessory cusp, the lowest and least developed of the four. Butler (1973) has also suggested these homologies.

As in the holotype of *E. florencae*, M₁ is relatively generalized. The trigonid is only slightly splayed (less anteroposteriorly extended than in *E. shotgunensis*) but is more buccolingually compressed than in M₂ and M₃. The paraconid of M₁ is usually the weakest trigonid cusp, while the protoconid is the largest. In M₂ and M₃, the metaconid is usually the highest trigonid cusp and the paraconid remains small and low.

The mandible in *Elphidotarsius* is shallower than in *Carpodaptes* or *Carpolestes*.

Two specimens in the Rock Bench sample

(PU Nos. 17439 and 17736) reveal the upper cheek teeth of *Elphidotarsius*. The better of these, PU 17439, is a right maxillary fragment with P³-M³ and two alveoli anterior to P³ (Figs. 8, 34B). Each of the anterior alveoli held a single-rooted tooth, P², and C or possibly P¹. The latter was the smallest of the known upper teeth. P³ and P⁴ reveal new evidence pertinent to the origin and affinities of the Carpolestidae. They are unspecialized relative to their development in *Carpodaptes* and *Carpolestes*, but compare very closely in structure with P³⁻⁴ of *Pronothodectes*. The resemblance is striking and is indeed closer between *Elphidotarsius* and *Pronothodectes* than between the former and either of the other carpolestid genera. The similarities involve much of the dentition and are surely indicative of true relationship. They support the conclusion that the Carpolestidae and the Plesiadapidae shared a close common ancestor. It is emphasized, nonetheless, that certain features are present in P³⁻⁴ of *Elphidotarsius* that clearly foreshadow developments more fully manifested in *Carpodaptes* and *Carpolestes*.

P³ is substantially smaller than P⁴, and the latter and M¹ are subequal. Both P³ and P⁴ are pyriform in outline, considerably longer on the buccal side than lingually. Both are much shorter anteroposteriorly than in the two later genera. P³ has two buccal cusps, a prominent one about in the center of the buccal crest, and a smaller cusp behind it. A longitudinal crest lies just lingual to the middle of the tooth and bears one central cusp. Internal to this is a lingual shelf, unfortunately fractured anteriorly in the only known specimen, so the possible presence of a cusp there can be neither verified nor ruled out. There is a faint ectocingulum. P⁴ is larger and has (as in later carpolestids and *Pronothodectes*) three longitudinal sections (rows of cusps, or crests with one or more cusps). There are four buccal cusps. The most anterior is small, possibly homologous with the parastyle. Behind it, located at approxi-

TABLE 1. METRICAL DATA FOR LOWER CHEEK TEETH OF *ELPHIDOTARSIVS*, CF. *E. FLORENCAE*, FROM ROCK BENCH QUARRY, POLECAT BENCH FORMATION.

		N	OR (mm)	\bar{x}	s	V
P ₄	length	16	1.7–1.9	1.79 ± .02	.085 ± .015	4.8 ± .8
	breadth	15	1.3–1.6	1.40 ± .03	.107 ± .020	7.6 ± 1.4
M ₁	length	15	1.4–1.6	1.50 ± .01	.038 ± .007	2.5 ± .5
	breadth	14	1.3–1.6	1.44 ± .02	.093 ± .018	6.5 ± 1.2
M ₂	length	15	1.3–1.6	1.41 ± .02	.083 ± .015	5.9 ± 1.1
	breadth	15	1.4–1.7	1.50 ± .02	.093 ± .017	6.2 ± 1.1
M ₃	length	11	1.8–2.1	1.95 ± .02	.082 ± .017	4.2 ± .9
	breadth	10	1.2–1.4	1.29 ± .02	.074 ± .017	5.7 ± 1.3
Mandibular depth		14	2.8–3.5	3.12 ± .05	.197 ± .037	6.3 ± 1.2

mately the center of the crest, is a prominent cusp (paracone?), followed by another well-developed cusp (metacone?). The last cusp on the buccal crest is much smaller and may be homologous with the metastyle. A central, longitudinal, crescentic ridge bears one large cusp anteriorly. Internal to this, a well-expressed cusp rises anteriorly from the lingual cingulum and is followed by a slight rise of enamel, probably an incipient hypocone. There is an ectocingulum, and anterolingual and posterolingual cingula are joined internally by the lingual cingulum.

The upper molars deviate little from the primitive plesiadapid pattern. They are very similar morphologically to the molars in other carpolestids, which have been thoroughly described by previous authors (Jepsen, 1930; Simpson, 1937a). The three trigon cusps are high and prominent; the paraconule and metaconule are smaller but distinct. A cingular hypocone, connected to the protocone by a "nannopithec fold", is well expressed on M¹ and M² but is virtually absent from M³. Pronounced cingula are present on the external, anterior, and posterior borders, except on M³, where the postcingulum is restricted to the lingual half of the tooth. The molars decrease in size from M¹ to M³, and in M³ the posterobuccal corner (metacone area) is greatly reduced. The molars in PU 17439 are more buccolingually distended than in many specimens of other carpolestids.

If the allocation of the Rock Bench Quarry sample to *E. florencae* is correct, speculations can be offered regarding the apparent size discrepancy between specimens in this sample and the holotype. The holotype may represent an unusually small individual, or, more probably, the Gidley Quarry population was, on the whole, slightly smaller than that of Rock Bench. Such differences in local populations are not uncommon in Recent species and should be expected in extinct species as well. Furthermore, although Gidley Quarry and Rock Bench are spatially and temporally close, there may be a slight age difference. The *Elphidotarsius* specimens now known suggest that Gidley Quarry is slightly older, and plesiadapid fossils strengthen this view (P. D. Gingerich, personal communication), although Sloan (1969; fig. 5) considered Rock Bench to be the earlier of the two.

To summarize, the Rock Bench Quarry sample of *Elphidotarsius* is best referred to *E. florencae*. The possibility cannot be dismissed, however, that additional specimens from Gidley Quarry or an equivalent level nearby could reveal sufficient distinctions from the Rock Bench population to warrant specific separation for the latter.

Three specimens (PU Nos. 16916, 19764, and 19780) from the Medicine Rocks (Tongue River Formation) near Ekalaka, Montana, are also tentatively referred to

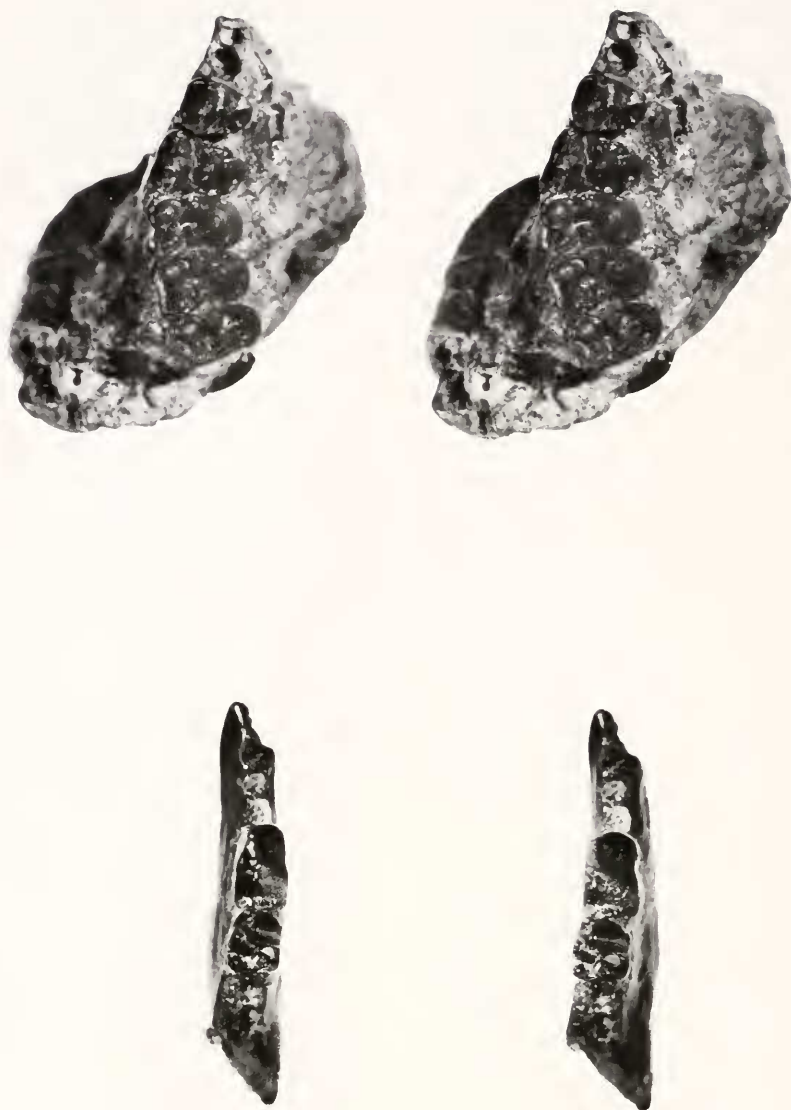


Figure 8. Above: *Elphidotarsius*, cf. *E. florencae* Gidley, PU 17439, right maxilla with P^3 - M^3 . Crown view. $\times 6$. Rock Bench Quarry. Below: *Elphidotarsius shotgunensis* Gazin, holotype, AMNH 88311, right P_4 - M_1 . Crown view. $\times 6$.

E. florencae. All are fragmentary mandibles with partial dentition, but only one specimen, PU 19764, preserves all of P_4 . In P_4 of this specimen, the presumed homologues of the molar trigonid cusps are prominent, with both paraconid and meta-

conid situated slightly lingual to the protoconid. The fourth, anteriormost cusp is much lower and very small, smaller than in other specimens referred to *E. florencae*. Whether this feature is significant taxonomically is unclear at present; PU 19764 is

otherwise like the holotype and the Rock Bench specimens.

Elphidotarsius shotgunensis Gazin, 1971
Figures 4C, 8

Elphidotarsius shotgunensis Gazin, 1971: 33.

Holotype: AMNH 88311, right mandibular fragment with P_4 - M_1 and anterior alveoli.

Hypodigm: Type and MCZ 18775,¹ a right M_1 .

Horizon and Locality: Late Middle Paleocene (late Torrejonian), Shotgun Member, Fort Union Formation: near Cottonwood Creek, Sect. 30-31, T. 6 N., R. 3 E., Wind River Basin, Wyoming.

Diagnosis (modified after Gazin): P_4 longer and narrower than in *E. florencae*; M_1 narrower than in *E. florencae*. Primary portion of P_4 with 4 apical cusps, possibly less well defined than in *E. florencae*. Trigonid of M_1 more elongate than in *E. florencae*, i.e., paraconid and metaconid more widely separated, but both lingually placed with respect to protoconid.

Discussion: Gazin described this form thoroughly, and there is no new material since his study to contribute further information. A re-examination of the type mandible, however, results in a different interpretation of the anterior dentition. The three alveoli immediately anterior to P_4 probably held P_3 , P_2 , and the canine. Anterior to the canine, Gazin suggests the presence of three incisors. This is very unlikely, for no known Paleocene primate had three lower incisors. The most anterior alveolus is enlarged and anteriorly inclined, as in other carpoolestids. It is followed by a smaller alveolus, for I_2 . Gazin interpreted a groove behind this as possibly the alveolus of a third incisor, but the groove is small and poorly defined, and it appears to be situated at a break in the mandible. It is most improbable that it represents an alveolus. (It should be noted that Gazin was duly hesitant in suggesting the presence of three incisors.) Specimens

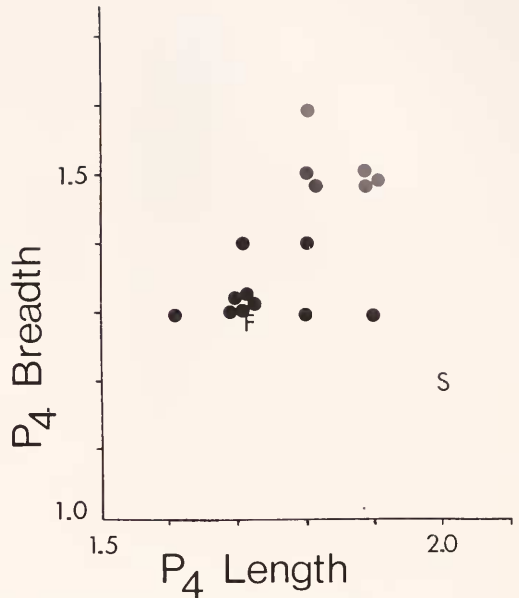


Figure 9. Scatter diagram of P_4 dimensions of *Elphidotarsius*. Black circles = *E.*, cf. *E. florencae* from Rock Bench Quarry. F = *E. florencae*, holotype, from Gidley Quarry. S = *E. shotgunensis*, holotype.

of *Elphidotarsius* from Rock Bench Quarry, discussed above, indicate the presence of only two lower incisors.

Gazin referred an upper premolar, MCZ 18774, to this species. Inspection of the specimen and comparison with other carpoolestids reveals that it is a very water-worn premolar of *Carpodaptes*, also known from this locality. With the elimination of this specimen, the known teeth of *E. shotgunensis* are reduced to P_4 and M_1 . Nevertheless, the morphology of these two is clearly more advanced than in *E. florencae* and suggests a trend toward *Carpodaptes*.

Carpodaptes Matthew and Granger, 1921

Carpodaptes Matthew and Granger, 1921: 6; Simpson, 1935: 10; Dorr, 1952: 82.

Type Species: *Carpodaptes aulacodon* Matthew and Granger, 1921.

Included Species: *C. aulacodon*, *C. hazelae*, *C. hobackensis*, *C. cygneus*, and *C. jepseni* (new species).

¹ This specimen has apparently been lost.

Distribution: Late Middle Paleocene (late Torrejonian) of Wyoming, Late Paleocene (Tiffanian) of western North America: Alberta, Saskatchewan, Montana, North Dakota, Wyoming, and Colorado.

Emended Diagnosis: Lower dental formula 2.1.2.3. Enlarged medial incisor longer and more slender than in *Elphidotarsius*. Lateral incisor ($I_2^?$), C , and P_3 reduced to tiny, single-rooted vestiges with buttonlike crowns. P_2 absent. P_4 larger, both relatively and absolutely, than in *Elphidotarsius*, but smaller in both respects than in *Carpolestes*; apical cusps numbering 5 or 6, followed by talonid heel less distinct than in *Elphidotarsius*, but generally more distinct than in *Carpolestes*; heel decidedly lower than trigonid of M_1 ; slight constriction of enamel at crown separating talonid from primary blade. Trigonid of M_1 elongate and open, paraconid immediately anterior or slightly anterolingual to protoconid; protoconid the most prominent trigonid cusp. M_{2-3} not significantly different from those of *Elphidotarsius* and *Carpolestes*, but third lobe of M_3 usually larger than in *Elphidotarsius*; incipient mesoconid sometimes present on cristid obliqua of M_3 . Upper dentition with at least two reduced teeth anterior to P^3 (presumably P^2 and C); both with one major cusp. P^{3-4} pyriform, polycusate, greatly enlarged over those of *Elphidotarsius*, but not so large as in *Carpolestes*. P^3 and P^4 subequal, or P^3 slightly smaller than P^4 , both larger than molars; each with 3 well-developed longitudinal rows of cuspules, buccal row longest. P^3 without pronounced anteroexternal spur typical of *Carpolestes*; external row with 4 cusps, the most anterior separated somewhat from the 3 posterior; median row a crescentic crest, with one or more cuspules, situated slightly buccal to middle of tooth; lingual section with two subequal cusps. P^4 with buccal row of 5 or 6 cusps, the 2 anterior ones separated slightly from the 3 or 4 posterior ones; median crest similar to that of P^3 ; lingual region with 3

cusps, the central cusp largest. Molars very similar morphologically to those of other carpolestid genera.

Carpodaptes aulacodon Matthew
and Granger, 1921

Figures 10, 11A

Carpodaptes aulacodon Matthew and Granger, 1921: 6; Simpson, 1935b: 12.

Holotype: AMNH 17367, left mandible with P_2 - M_3 .

Hypodigm: Type specimen only.

Horizon and Locality: Late Paleocene (Tiffanian), Tiffany Formation: Mason Pocket, Tiffany, Colorado.

Emended Diagnosis: P_4 bearing 5 poorly-defined apical cusps, followed by distinctly separated, low talonid heel; anteriormost cusp almost indistinct, as low as talonid and separated somewhat from following 4 closely appressed cusps; lateral profile roughly triangular with apex almost pointed, in contrast to more gently rounded profiles of P_4 in other species of *Carpodaptes*. P_4 longer than in *C. hazelae*, *C. hobackensis*, or *C. cygneus*, shorter than in *C. jepseni* or species of *Carpolestes*. Molars not significantly different from those of other species.

Discussion: This revised diagnosis of *Carpodaptes aulacodon* is the first published since other species were added to the genus. The type mandible clearly reveals the great reduction of the teeth between the enlarged incisor and P_4 , a characteristic of carpolestids which is manifested to a greater degree in *Carpolestes* and *Carpodaptes* than in *Elphidotarsius*.

The structure of P_4 , the most diagnostic mandibular tooth in carpolestids, differs from that of all other species of *Carpodaptes*, and we may be confident (despite the existence of only one specimen) in recognizing AMNH 17367 as a representative of a distinct species.

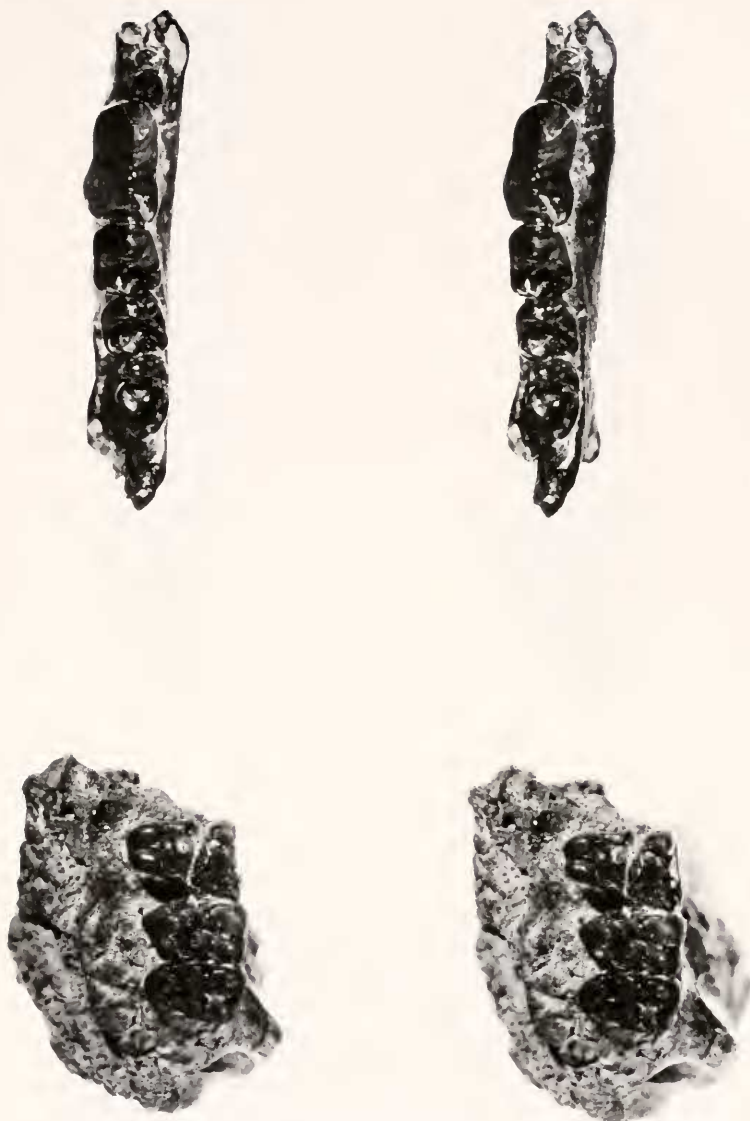


Figure 10. Above: *Carpodaptes aulacodon* Matthew and Granger, holotype, AMNH 17367, left P_3 - M_3 . Crown view. $\times 6$. Below: *Carpodaptes* sp., PU 14639. Left maxilla with P^4 - M^2 , crown view. $\times 6$.

Carpodaptes hazelae Simpson, 1936
Figures 11C, D, 12-18

Carpodaptes hazelae Simpson, 1936: 21; Simpson, 1937a: 5.

Holotype: AMNH 33854, right mandible with P_4 - M_3 .

Hypodigm: Type and AMNH Nos. 33853, 33855, 33887, 33979-33985, from Scarritt Quarry; PU Nos. 19558, 19572, 19574, 19596, 19601, 19936, 19939, 19953-19955, 19958, 19968, 19969, 19985, 20007, 20010, 20011, 20034, 20060, 20064, 20065, 20068, 20084, 20087, 20610, 20615, 20630, 20634, 20656, 20719, 20808, 20812, 20820, 20839, 20840,

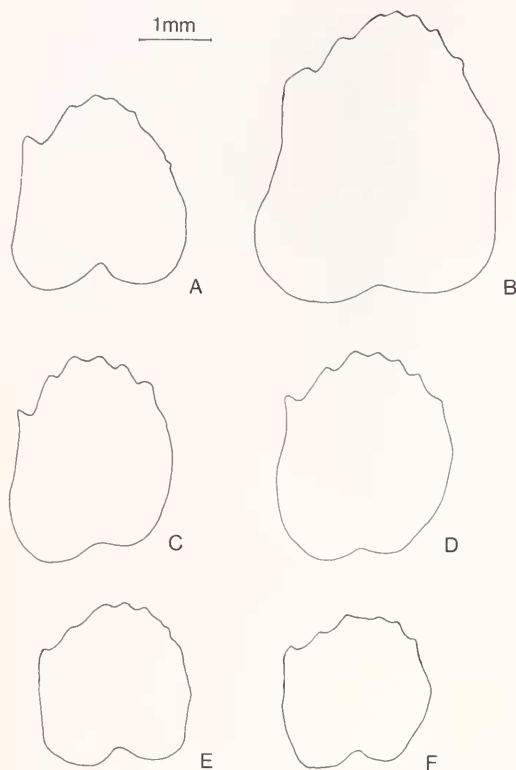


Figure 11. Outlines of right P_4 of *Carpodaptles* (lateral aspect), to same scale. A) *C. aulacodon*, holotype, AMNH 17367 (reversed). B) *C. jepseni*, holotype, PU 20716. C) *C. hazelae*, holotype, AMNH 33854 (Scarritt Quarry). D) *C. hazelae*, PU 20084 (Cedar Point Quarry). E) *C. hobackensis*, UMMP V55124. F) *C. cygneus*, holotype, ROM 05622.

20886, 20889, 20898, 20900, 21213, 21266, 21279, 21297, 21299, 21316, 21317, 21330, 21341, 21350, 21351, 21357, 21384, 21393, 21399, 21413, 21419, 21437, 21438, from Cedar Point Quarry.

Horizon and Locality: Late Paleocene (Tiffanian) of Montana and Wyoming: Scarritt Quarry, Melville Member, Fort Union Formation, Crazy Mountain Field, Montana; Cedar Point Quarry, Polecat Bench Formation, Big Horn County, Wyoming.

Emended Diagnosis: Close to *C. aulacodon* in size, but mean length of P_4 less than in *C. aulacodon*. P_4 with 5 or 6 variably defined apical cusps followed by a low but distinct talonid heel; more rounded in profile and more quadrate in occlusal

view (at base) than in *C. aulacodon*. Molars not significantly different morphologically from other species, but larger than in *C. hobackensis* and *C. cygneus*, smaller than in *C. jepseni*.

Discussion: *Carpodaptles hazelae* was originally described and defined from a small sample collected at the Scarritt Quarry in the Crazy Mountain Field. The much larger sample from Cedar Point Quarry is here referred to *Carpodaptles hazelae* and necessitates the revised diagnosis presented above. *C. hazelae* is now represented by more specimens than any other species of the family.

There can be little doubt that the carpolestids from Cedar Point Quarry all represent the same species. Although considerable variation is observed, graphs of tooth dimensions reveal normal, unimodal distribution; there is no indication of sexual dimorphism and no evidence of the presence of more than one taxon. Since the different variations do not fall into consistently distinct groups, there is no practicable method of distinguishing more than one species, and indeed, no justification for so doing. On the other hand, a casual examination of some of the specimens here referred to *C. hazelae* might suggest that the Cedar Point Quarry sample represents a species distinct from that of Scarritt Quarry. But, as noted above, separate populations of a species not uncommonly show minor differences, and this should not be unexpected in *C. hazelae*. The large sample of this species now known provides us with a good cross-section of the variation which may occur intraspecifically in carpolestids, and it is substantial. But almost all variation is limited to the specialized premolars, P_4 and P_3-4 . Although some specimens in the Cedar Point sample differ in size or in minor morphologic details from the type specimen (from Scarritt Quarry), others are virtually identical to the type. The Scarritt Quarry specimens tend to be slightly larger and their lower cheek teeth (P_4-M_3) relatively broader than the mean

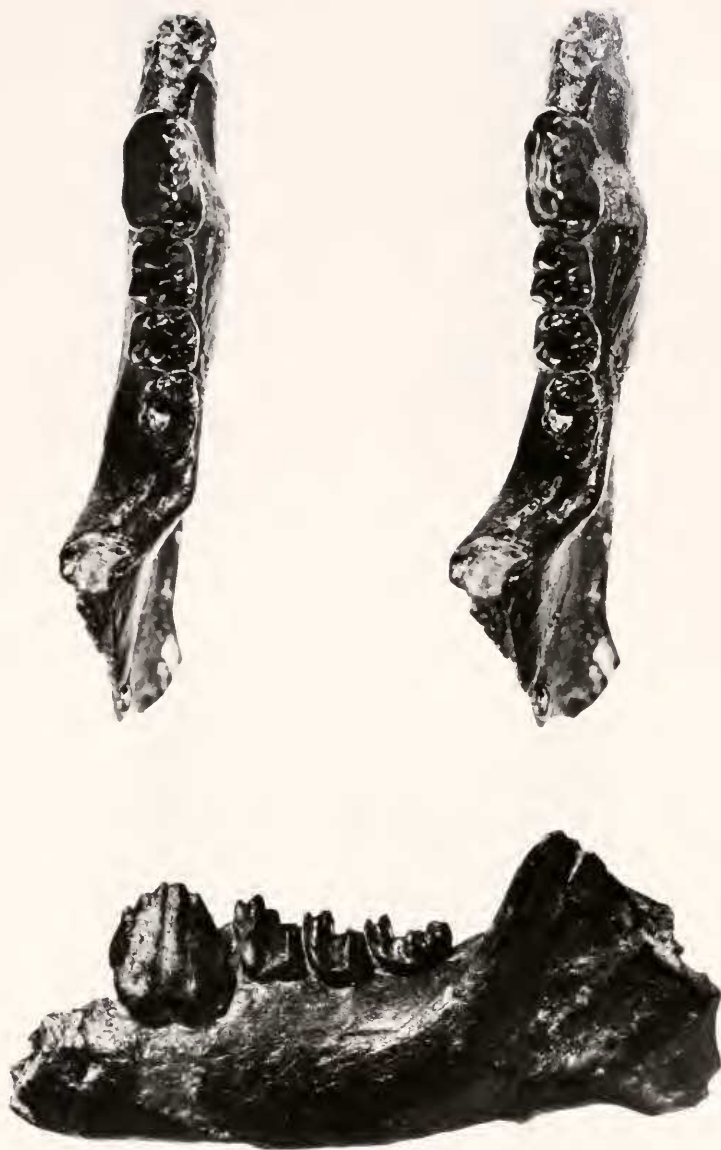


Figure 12. *Carpodectes hazelae* Simpson, AMNH 33980, left dentary with P_4 - M_3 . Crown view (above) and lateral view (below). $\times 6$. Scarritt Quarry.

values for the Cedar Point sample, but several Cedar Point specimens exceed in size even the largest Scarritt specimen. P_4 in the best preserved individuals from Scarritt Quarry bears 5 sharp, relatively large apical cuspules followed by a lower, distinct

talonid heel (Fig. 12). In the Cedar Point specimens, the apical cuspules, 5 or 6 in number, are usually (but not always) less well defined (Fig. 16). The sixth cuspule arises low at the anterior of the blade in about 75% of the known specimens (44 of

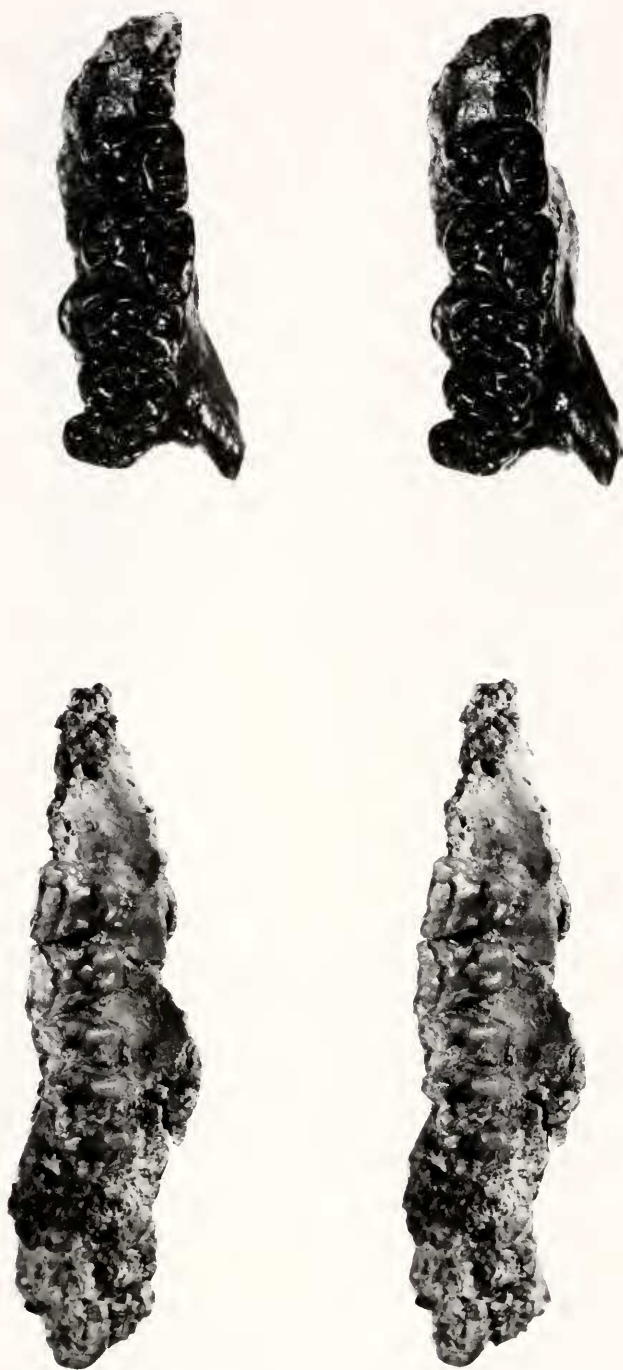


Figure 13. Above: *Carpodaptes hazelae* Simpson, AMNH 33980, left maxilla with P²-M³. Crown view. $\times 6$. Scarritt Quarry. Below: *Carpodaptes hazelae* Simpson, PU 19939, right maxilla with P³-M³, crown view. $\times 6$. Cedar Point Quarry.



Figure 14. *Carpodectes hazelae* Simpson, PU 20839, right dentary with P_4 - M_3 . Crown view (above) and lateral view (below). $\times 6$. Cedar Point Quarry.

59 specimens); it is variably developed, ranging from an incipient cuspule to one as well defined as any of the other apical cusps. The talonid of P_4 in the Cedar Point specimens is usually not so distinctly set off from the blade as in the Scarritt individuals, but this feature, too, is variable.

Only a few upper dentitions are known for *Carpodectes hazelae*. The Scarritt Quarry and Cedar Point Quarry specimens are similar except for the position of one

cusp on P^1 (Fig. 18). In the lingual section of P^1 in three Scarritt specimens, the central cusp (the largest of the three lingual cusps) is situated approximately between the other two lingual cusps and contributes to the lingual face of the tooth. This same cusp in the two known specimens from Cedar Point is situated posterolabial to the anteriormost lingual cusp, thus it contributes almost nothing to the lingual face of the tooth. The fourth Scarritt specimen

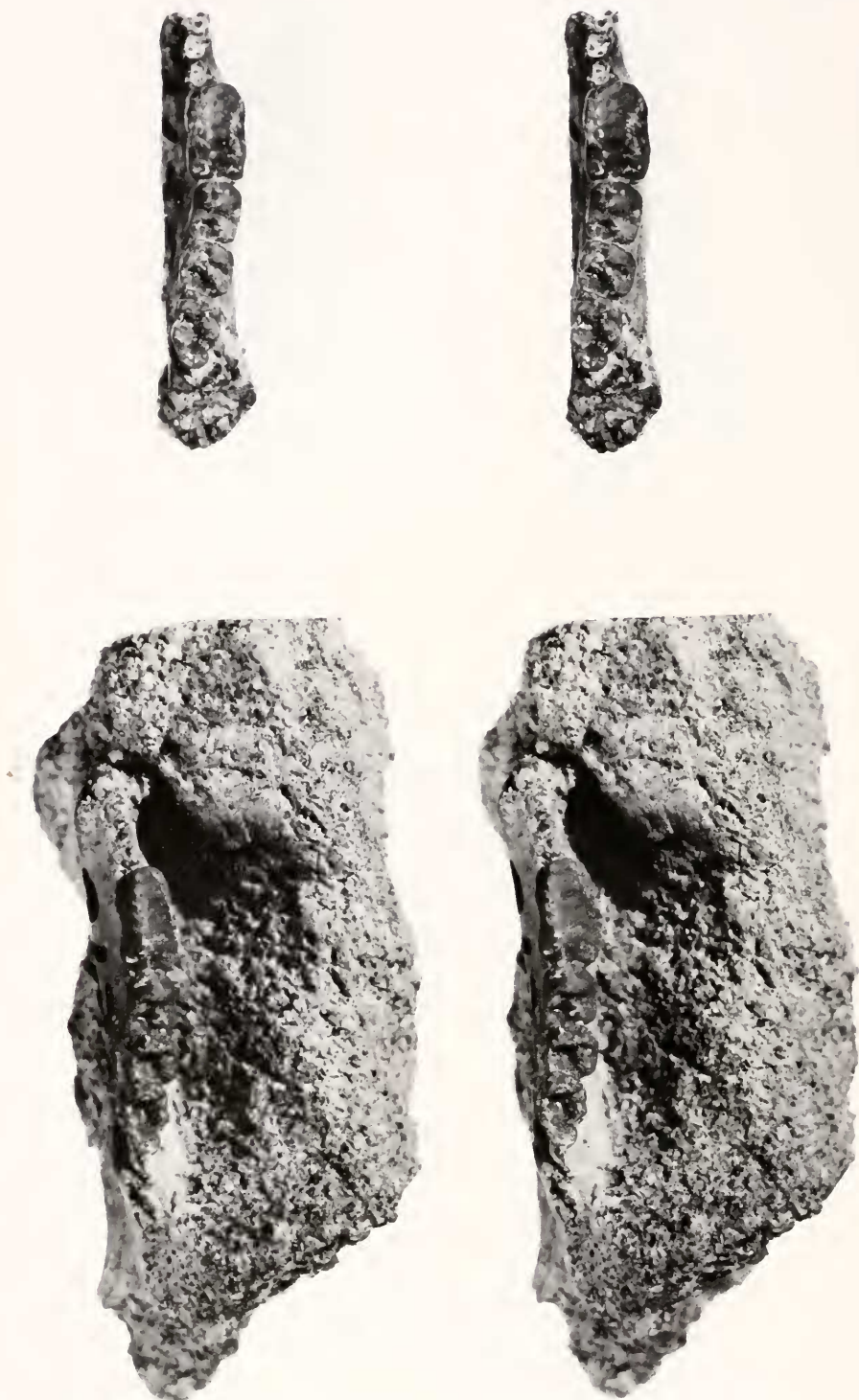


Figure 15. *Carpodaptes hazelae* Simpson. Above: PU 21350, right dentary with P_4-M_3 , crown view. Below: PU 21351, right dentary with P_4-M_3 , crown view. $\times 6$. Cedar Point Quarry.

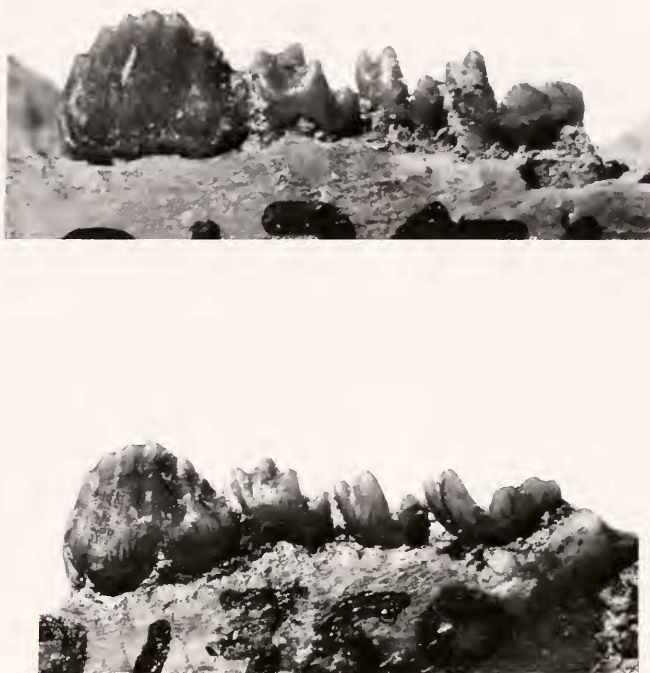


Figure 16. *Carpodaptes hazelae* Simpson. Above: PU 21351, right dentary with P_4 - M_3 , medial view. Note presence of 6 apical cusps. Below: PU 21350, right dentary with P_4 - M_3 , medial view. Note presence of 5 apical cusps. Both $\times 6$. Both from Cedar Point Quarry.

preserving P_4 (AMNH 33981) is nearly intermediate between these two morphologies, suggesting that the difference is not taxonomically significant.

In addition to the Scarritt Quarry and Cedar Point Quarry remains referred to this species, there are a few specimens from the Late Torrejonian Shotgun Local Fauna (MCZ Nos. 18763, 18776, 18777, 19683, 19684) that are closely comparable to *C. hazelae*. They are the earliest recorded representatives of the genus *Carpodaptes*, and the only ones known from pre-Tiffanian sediments.

An isolated P_4 (UMVP 5007) from the Circle Local Fauna, Tongue River Formation, near Circle, Montana, is probably referable to *C. hazelae*.

Specimens of *Carpodaptes* from the Ravenscrag Formation in Alberta were referred to *Carpodaptes*, cf. *C. hazelae*, by

Krishtalka (1973), although (as he noted) they are smaller than typical *C. hazelae*. They are closer in size and morphology to *Carpodaptes cygneus* and are here tentatively referred to the latter.

The dental morphology of *C. hazelae* has been described in detail by Simpson (1936, 1937a). No new material has been recovered from Scarritt Quarry since Simpson's work, and the material he described in 1937 still includes some of the most complete carpolestid specimens known. Among the Cedar Point specimens are several which preserve the anterior portion of the mandible, but only alveoli are preserved anterior to P_3 . From these specimens it is clear that there were three diminutive, single-rooted teeth between the large medial incisor and P_4 . I interpret these as a lateral incisor, the canine, and P_3 . P_3 is preserved in only one specimen, PU

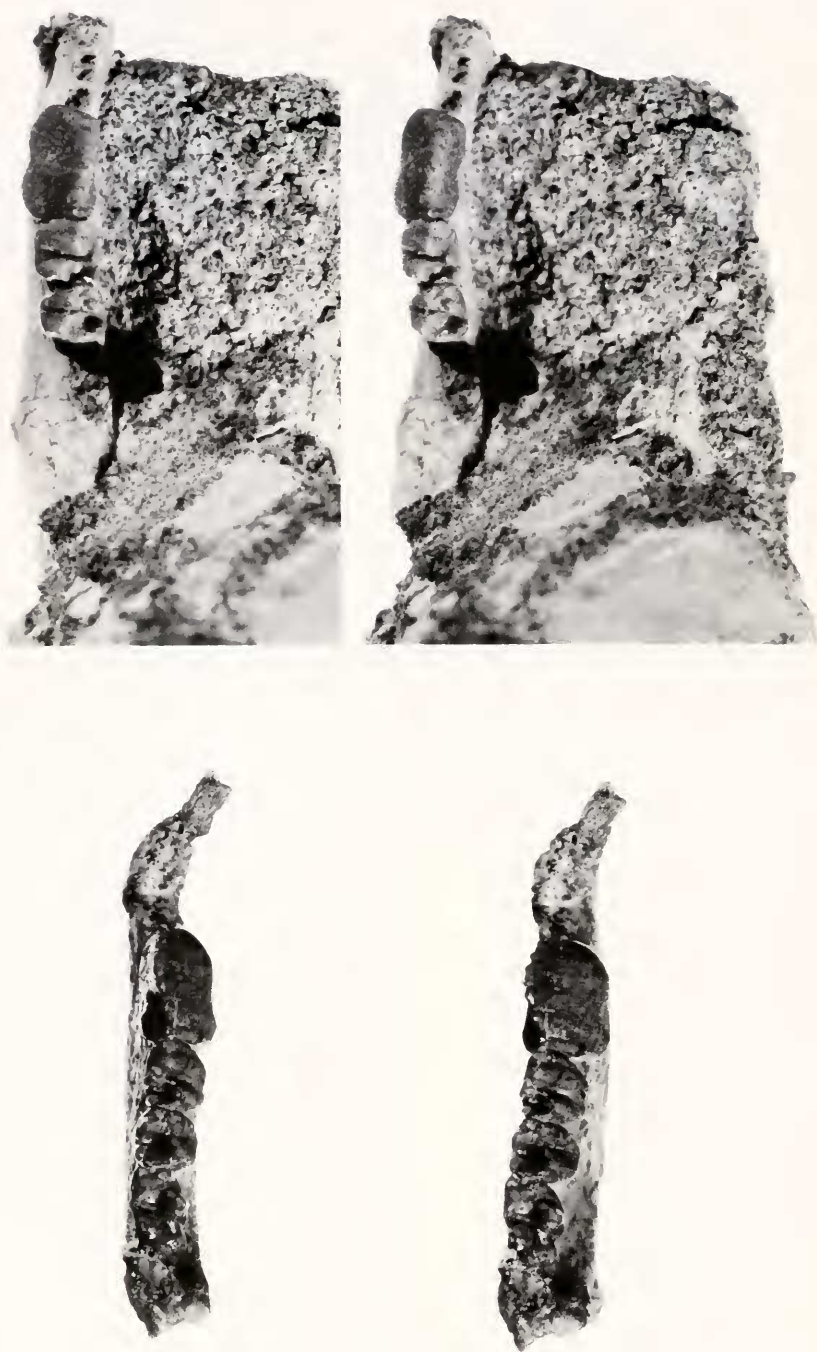


Figure 17. *Carpodectes hazelae* Simpson. Above: PU 21297, left dentary with P_4 - M_2 , crown view. Below: PU 20084, right dentary with P_4 - M_3 , crown view. Both $\times 6$. Both from Cedar Point Quarry.

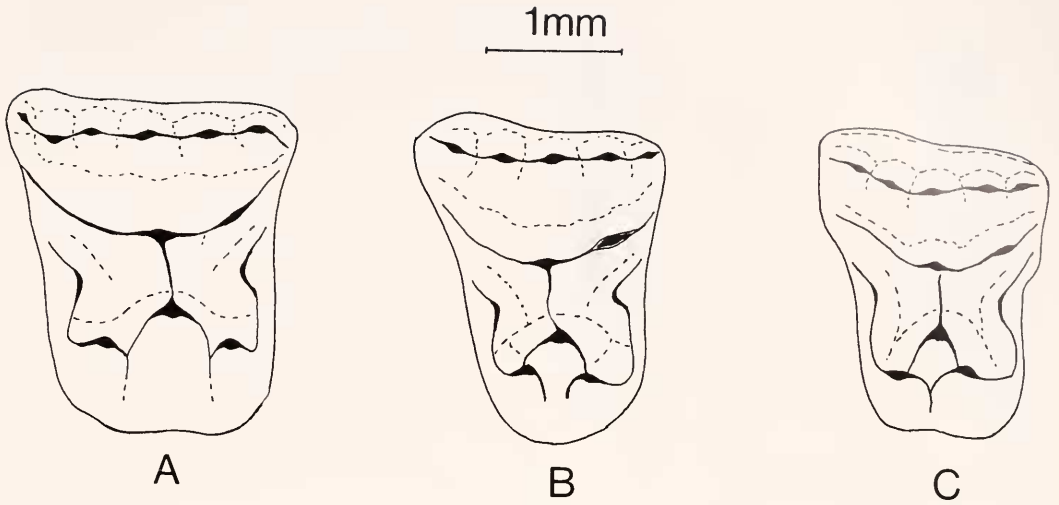


Figure 18. Crown view of right P_4 of *Carpodartes hazelae*, to same scale. A) AMNH 33980 (reversed), from Scarritt Quarry. B) AMNH 33981, from Scarritt Quarry. C) PU 19939, from Cedar Point Quarry.

20630, and is much reduced compared to that of *Elphidotarsius*. It is a vestigial peg-like tooth, with the same morphology as P_3 in *C. aulacodon* (and similar, in fact, to P_3 in *Carpolestes*). The morphology of P_4 has been discussed above. It should be emphasized again that although P_4 is unquestionably the most diagnostic mandibular tooth in carpolestids, it is also the most variable. The extent of its variability is especially well demonstrated in the large sample of *C. hazelae*.

The molars (lower and upper) of the Cedar Point specimens are virtually indistinguishable from those of the Scarritt Quarry specimens. There is some variation, of course, in relative proportions (e.g., relative breadth of the lower molars).

A maxillary dentition (AMNH 33980) from Scarritt Quarry, described by Simpson (1937a), included two small, single-rooted teeth anterior to P^3 . Unfortunately, the anteriormost of these ($C^?$), unknown in any other carpolestid specimen, has been

TABLE 2. METRICAL DATA FOR LOWER CHEEK TEETH OF *CARPODARTES HAZELAE*, COMBINED SAMPLES FROM SCARRITT AND CEDAR POINT QUARRIES.

		N	OR (mm)	\bar{x}	s	V
P_4	length	56	2.1–2.8	$2.46 \pm .02$	$.142 \pm .013$	$5.8 \pm .5$
	breadth	55	1.2–1.8	$1.54 \pm .02$	$.134 \pm .013$	$8.7 \pm .8$
M_1	length	53	1.3–1.6	$1.47 \pm .01$	$.078 \pm .008$	$5.3 \pm .5$
	breadth	52	1.2–1.6	$1.34 \pm .01$	$.097 \pm .010$	$7.2 \pm .7$
M_2	length	39	1.1–1.4	$1.29 \pm .01$	$.070 \pm .008$	$5.4 \pm .6$
	breadth	39	1.2–1.6	$1.36 \pm .01$	$.091 \pm .010$	$6.7 \pm .8$
M_3	length	17	1.7–2.0	$1.86 \pm .02$	$.093 \pm .016$	$5.0 \pm .9$
	breadth	17	1.0–1.4	$1.18 \pm .02$	$.103 \pm .018$	8.7 ± 1.5
Mandibular depth		36	3.1–4.0	$3.49 \pm .04$	$.228 \pm .027$	$6.5 \pm .8$

TABLE 3. METRICAL DATA FOR LOWER CHEEK TEETH OF *CARPODAPTES HAZELAE* FROM CEDAR POINT QUARRY ONLY.

		N	OR (mm)	\bar{x}	s	V
P ₄	length	53	2.1–2.8	2.46 ± .02	.143 ± .014	5.8 ± .6
	breadth	52	1.2–1.8	1.53 ± .02	.132 ± .013	8.6 ± .8
M ₁	length	47	1.3–1.6	1.46 ± .01	.077 ± .008	5.3 ± .5
	breadth	46	1.2–1.5	1.32 ± .01	.087 ± .009	6.6 ± .7
M ₂	length	33	1.1–1.4	1.29 ± .01	.070 ± .009	5.4 ± .7
	breadth	33	1.2–1.5	1.34 ± .01	.079 ± .010	5.9 ± .7
M ₃	length	14	1.7–2.0	1.86 ± .03	.101 ± .019	5.4 ± 1.0
	breadth	14	1.0–1.3	1.16 ± .03	.094 ± .018	8.1 ± 1.5
Mandibular depth		33	3.1–4.0	3.46 ± .04	.221 ± .027	6.4 ± .8

lost since Simpson's description. Both P³ and P⁴ are hypertrophied and specialized in *C. hazelae*. P⁴ has 5 or 6 buccal cusps, the two anterior ones closely associated and separated slightly from the three or four posterior cusps. The specialization of P³ is especially dramatic in comparison to the small, generalized P³ of *Elphidotarsius*. Morphological details of P³ and P⁴ in *C. hazelae* have been listed above in the diagnosis of *Carpodaptes* and in Simpson's (1937a) description.

Carpodaptes hobackensis Dorr, 1952
Figures 11E, 19, 20A

Carpodaptes hobackensis Dorr, 1952: 82.

Holotype: UMMP 27233, left mandible with I₁, P₁-M₃, and roots of I₂, C, P₃.

Hypodigm: Type and UMMP Nos. 27234, 27253, 55124.

Horizon and Locality: Late Paleocene (Tiffanian), Dell Creek Local Fauna, Hoback Formation: UM-Sub-Wy Locality No. 1, Dell Creek Quarry, Sublette County, Wyoming.

Diagnosis (modified after Dorr, 1952): About the same size as *C. cygneus* but smaller than all other known species of *Carpodaptes*. P₄ lower and more gently rounded in lateral profile than in other species of *Carpodaptes*, except *C. cygneus*; crest S-shaped in occlusal view due to deep posterointernal excavation of tooth, bearing 5 small but distinct apical cusps and a talonid cusp; talonid not so clearly separated from main blade as in *C. hazelae* or *C. aulacodon*; incipient lower anterior

TABLE 4. METRICAL DATA FOR LOWER CHEEK TEETH OF *CARPODAPTES HAZELAE* FROM SCARRITT QUARRY ONLY.

		N	OR (mm)	\bar{x}	s	V
P ₄	length	4	2.5–2.6	2.58 ± .03	.050 ± .018	1.9 ± .7
	breadth	4	1.7	1.70	0	0
M ₁	length	7	1.4–1.6	1.51 ± .03	.069 ± .018	4.6 ± 1.2
	breadth	7	1.4–1.6	1.47 ± .03	.076 ± .020	5.1 ± 1.4
M ₂	length	7	1.2–1.5	1.34 ± .04	.098 ± .026	7.3 ± 2.0
	breadth	7	1.4–1.6	1.47 ± .03	.076 ± .020	5.1 ± 1.4
M ₃	length	4	1.8–2.0	1.90 ± .04	.082 ± .029	4.3 ± 1.5
	breadth	4	1.2–1.4	1.28 ± .05	.096 ± .034	7.5 ± 2.7
Mandibular depth		4	3.7–3.8	3.75 ± .03	.058 ± .021	1.5 ± .5

seventh cusp variable in occurrence; tooth very similar to that of *C. cygneus*, differing in having less pronounced vertical ribs developed beneath apical cusps on lingual side, less developed posterior apical cusp (cusp just anterior to talonid heel), and, consequently, a deeper posterolingual depression than in *C. cygneus*; weakly expressed posterointernal cingulum present, extending forward beyond midpoint of tooth. Weak internal cingulum at base of trigonid of M_1 .

Discussion: This species is very close to the subsequently described species *C. cygneus* (L. S. Russell). Specimens now known reveal minor but apparently consistent differences between the two, and both are accordingly retained as valid taxa in this review. They are so similar, however, that they must be very closely related, and it is not inconceivable that future evidence could provide justification for placing *C. cygneus* in synonymy.

Although only four specimens are known (no upper teeth have been recovered) the entire lower dentition is represented. The type mandible preserves parts or all of the lower teeth. The enlarged incisor unfortunately was damaged in preparation, but as restored it is a relatively longer and more slender tooth than in *Elphidotarsius*, much closer to the enlarged incisor of *Carpolestes*. This is the only incisor of *Carpodaptes* known, except for one isolated tooth from the Shotgun Local Fauna (UW 6530), possibly from *Carpodaptes* sp. (see Fig. 5B). Though only roots of the I_2 , C, and P_3 remain, their crown shapes are clearly indicated by impressions in the matrix. All were diminutive, single-rooted, peglike teeth with bulbous crowns.

P_4 , with its posterointernal depression, S-shaped crest, and talonid less distinctly separated from the main blade than in other species of *Carpodaptes*, bears a closer resemblance to P_4 of *Carpolestes* than does P_4 of any other species of *Carpodaptes*, except possibly *C. jepseni* (which in other ways foreshadows *Carpolestes*). For these



Figure 19. *Carpodaptes hobackensis* Dorr, UMMP V55124, right dentary with P_4 – M_3 . Crown view (above) and medial view (below). $\times 6$.

reasons Dorr (1952: 84) suggested indirectly that *C. hobackensis* might be closer to the ancestry of *Carpolestes* than any other species of *Carpodaptes* then known. The diminutive size of *C. hobackensis* relative to other species of *Carpodaptes* casts doubt on such a possible relationship, however.

No additional specimens have been recovered since Dorr's report. His thorough description obviates the need for further detail here.

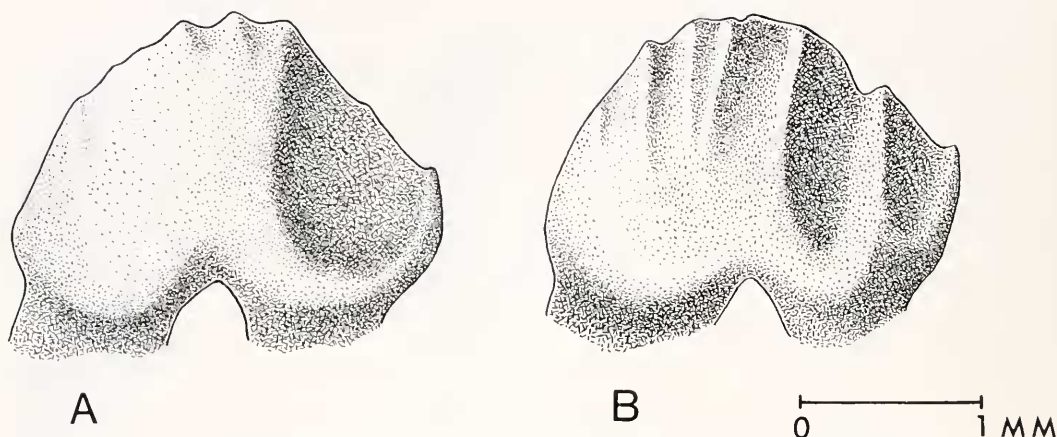


Figure 20. Lingual view of right P_4 of A) *Carpodectes hobackensis*, and B) *Carpodectes cygneus*.

Carpodectes cygneus (L. S. Russell),
1967

Figures 11F, 20B

Carpolestes cygneus L. S. Russell, 1967: 19.

Holotype: ROM 05622, right mandibular fragment with P_4 .

Hypodigm: Type and paratypes, ROM Nos. 05623 and 05624, from Swan Hills, Alberta; numerous specimens in the University of Alberta collection from near Roche Percee, Saskatchewan, including UA Nos. 8733, 8742, 8799, 8800.

Horizon and Locality: Late Paleocene (early [?] Tiffanian) of Alberta and Saskatchewan: Paskapoo Formation of the Swan Hills, north-central Alberta, and Ravenscrag Formation of southern Saskatchewan (and Alberta?).

Emended Diagnosis: Small carpoolestids near *Carpodectes hobackensis* in size but smaller than other known species. P_4 with 5 or 6 small apical cusps; posterior cusp (anterior to talonid cusp) well expressed; vertical ribs beneath apical cusps on lingual side pronounced, noticeably better developed than in *C. hobackensis*; postero-internal depression not as deep as in *C. hobackensis*.

Discussion: Russell named this species on the basis of three jaw fragments each holding a single tooth: two lower fourth premolars and one upper third premolar.

Fortunately, these are the most diagnostic teeth. Russell regarded the species as closest to *Carpolestes dubius* and cited the resemblances between the two as justification for allocating the new species to the genus *Carpolestes*. As Krishtalka (1973) pointed out, all the features noted by Russell are characteristic of *Carpodectes*; there is no special resemblance to *Carpolestes*. In fact, *C. cygneus* is remarkably close to *C. hobackensis*, a form described fifteen years earlier. The only noticeable differences in the dentition as known occur in P_4 ; these have been detailed above under *C. hobackensis* (See also Fig. 20).

A large sample recently recovered from the Ravenscrag Formation of Saskatchewan by D. Krause (personal communication) is referable to *C. cygneus*. Many specimens are considerably more complete than Russell's original lot and show the mandibular dentition, other than P_4 , to be virtually indistinguishable from that of *C. hobackensis*. A thorough description of these will be published by Krause.

P^3 , known from one of the paratypes (ROM 05624) and a few of Krause's specimens, shows some distinctions from that of *C. hazelae* (the only other species of the genus in which upper teeth are known). ROM 05624 is smaller and more square in

occlusal view than P^3 of *C. hazelae*. In the posterior third of the tooth there is a short invagination of the posterior wall in the form of a crest roughly parallel to, and between, the median and lingual cusp rows. This crest is present also in UA 8799, from the Ravenscrag of Saskatchewan (but this tooth is closer in shape to that of *C. hazelae* than to ROM 05624).

Krishtalka (1973) referred a sample from the Ravenscrag of Alberta to *Carpodaptes*, cf. *C. hazelae*. In size and P_4 morphology, the specimens are more like *C. cygneus* than *C. hazelae*, and are here designated *Carpodaptes* sp., cf. *C. cygneus*. One of these is a P^3 (UA 5857) which lacks the crest observed in ROM 05624 and UA 8799.

Also allocated tentatively to *C. cygneus* are a few isolated teeth (UMVP collection, uncatalogued) from Tiffanian deposits of the upper Tongue River Formation at Olive, Montana.

R. C. Holtzman (personal communication) has recently collected specimens of *Carpodaptes* from the lower part of the Tongue River Formation near Judson, North Dakota (UMVP Nos. 6062, 6063, 6142, 6190, 6217, 6355, 6517, and 6518). They show resemblances to both *C. cygneus* and *C. hobackensis*. UMVP Nos. 6062 and 6142 lack the prominent lingual ridge beneath the last apical cusp of P_4 , a characteristic of *C. cygneus*, consequently showing the posterolingual hollowing typical of *C. hobackensis*. On the other hand, UMVP Nos. 6063 and 6190, in which the ridge is well developed in P_4 , are like *C. cygneus*. The Judson sample may represent the sympatric occurrence of the two species, but suggests that they may be synonymous. Description of the specimens is in preparation by Holtzman.

Carpodaptes jepseni, new species Figures 11B, 21

Etymology: Named for the late Professor Glenn Lowell Jepsen, in recognition of his outstanding contributions to our knowledge of Paleocene

mammals, and in particular for his efforts in the recovery of the majority of known carpo-
lestid specimens.

Holotype: PU 20716, right mandible with P_4 - M_2 .

Hypodigm: Type specimen only.

Horizon and Locality: Late Paleocene (Tiffanian), Polecat Bench Formation: Divide Quarry, NE 1/4, SW 1/4, Sect. 16, T. 54 N., R. 95 W., Big Horn County, Wyoming.

Diagnosis: Largest known species of *Carpodaptes*, about the size of *Carpolestes nigridens* and *dubius*. P_4 very high crowned, bearing 6 well-developed apical cusps followed by lower, separate talonid heel; last apical cusp lower but better developed than those anterior to it, as in *C. cygneus*; talonid lower than trigonid of M_1 , and distinctly separated from main blade as in *C. hazelae* and *C. aulacodon*; lateral profile close to that of *C. aulacodon*, approaching a more pointed form than in other species. Paraconid of M_1 only slightly subordinate to protoconid. Molars longer and broader than in other species.

Discussion: This problematical specimen shows features which resemble both *Carpodaptes* and *Carpolestes*, but it does not fit very conveniently into either. The balance of features, however, seems to weigh in favor of *Carpodaptes*, to which it is here referred. At present, this is preferable to a proposal of a new genus.

The number and clarity of the apical cusps of P_4 are characteristic of *Carpodaptes*, as are the well-developed sixth apical cusp and the distinctly lower and well separated talonid cusp. These features are not found in *Carpolestes*. On the other hand, the large size, high crown, and the relative size of P_4 to the molars are much more like *Carpolestes*. The species could therefore be regarded either as a less specialized representative of *Carpolestes* or as a large, relatively advanced representative of *Carpodaptes*.

The age of Divide Quarry is not yet well established, but it appears to be later than



Figure 21. *Carpodaptes jepseni*, new species, holotype, PU 20716, right dentary with P_4 – M_2 . Crown view (above) and medial view (below). $\times 6$.

Cedar Point Quarry, which yields *Carpodaptes hazelae*, and earlier than Princeton Quarry, which yields *Carpolestes dubius* (D. C. Parris, *in litt.*, 2/18/72). It appears, then, that *C. jepseni* is both structurally and stratigraphically intermediate between *Carpodaptes* and *Carpolestes*. It is probably in or very near the ancestry of *Carpolestes*.

The posterior portion of a P_4 (PU 20852) from Long Draw Quarry, Carbon County, Montana, is possibly referable to *C. jepseni*.

Carpodaptes sp.

Figure 10

A maxillary fragment (PU 14639) from Princeton Locality 11 in the Crazy Mountain Field, Montana, preserves left P^1 – M^2 . It is close in size to *Carpodaptes hazelae*, but P^1 is more triangular (lingually compressed) and relatively more extended buccolingually than in *C. hazelae*. In the orientation of the three lingual cusps of P_4 , PU 14639 resembles the Cedar Point speci-

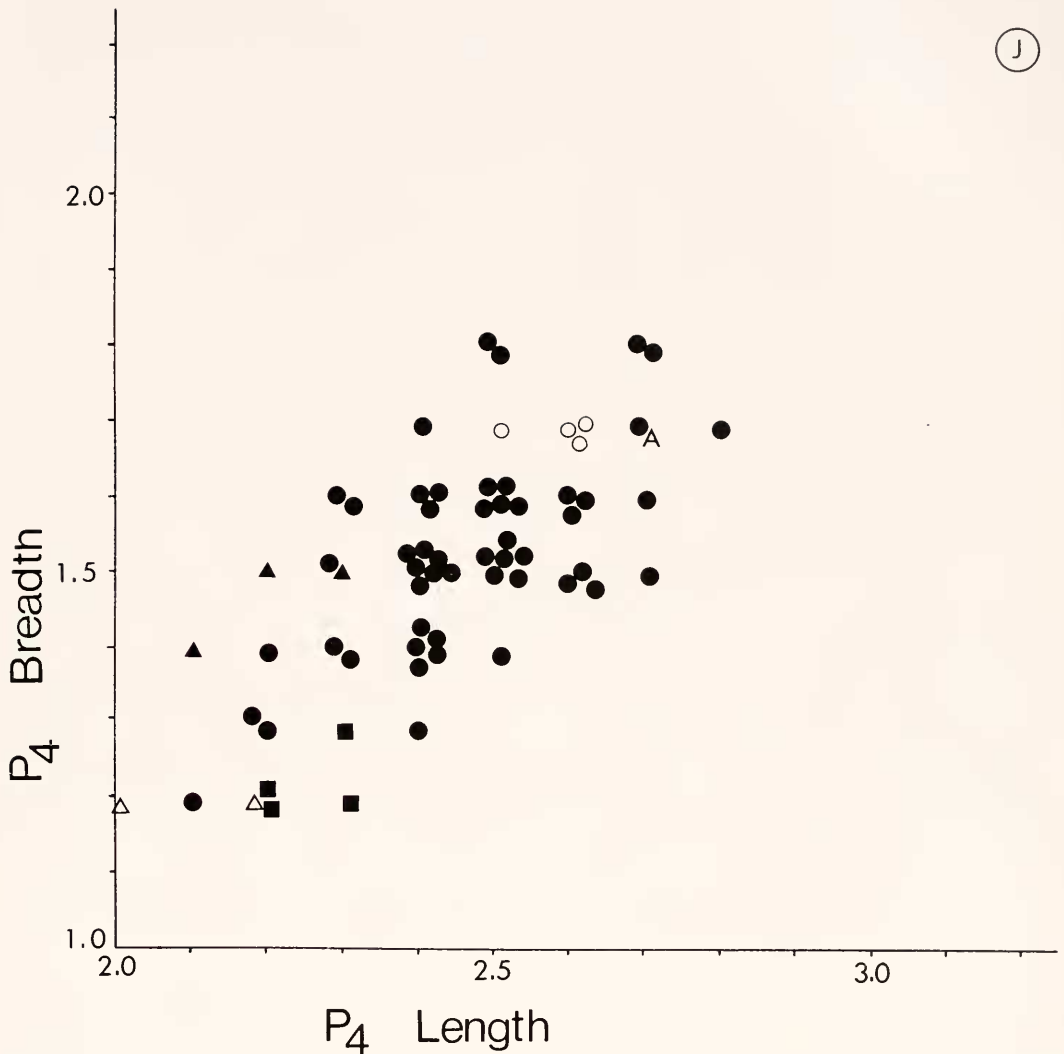


Figure 22. Scatter diagram of P_4 dimensions of *Carpodaptus*. Black circles = *C. hazelae* from Cedar Point Quarry. Open circles = *C. hazelae* from Scarritt Quarry. Black squares = *C. hobackensis*. Open triangles = *C. cygneus* from Swan Hills. Black triangles = *C.*, cf. *C. cygneus* from Cypress Hills, Alberta. A = *C. aulacodon*, holotype. Circled J = *C. jepseni*, holotype.

mens more closely than those of Scarritt Quarry. Locality 11 (Simpson, 1937b: 41) is approximately 1000 feet stratigraphically above the Scarritt Quarry, thus it is possible that this specimen represents a hitherto undescribed species. Bell (1941), in an unpublished thesis, based a new species on

PU 14639. In view of the small number of maxillary dentitions known for this genus, and the high degree of intraspecific variability present in large samples (of lower teeth, for example) it seems more appropriate for the present to refer this to *Carpodaptus* sp. than to propose a new taxon.

Carpolestes Simpson, 1928*Carpolestes* Simpson, 1928: 7.*Litotherium* Simpson, 1929: 9.Type Species: *Carpolestes nigridentis* Simpson, 1928Type Species of Synonym: *Litotherium complicatum* Simpson, 1929.Included Species: *C. nigridentis* and *C. dubius*.

Distribution: Latest Paleocene ("Clarkforkian") and earliest Eocene (Wasatchian) of Montana and Wyoming.

Emended Diagnosis: Largest, most specialized carpolestids. Dental formula $\frac{2.2.1.3}{2.1.2.3}$. Anterior lower dentition much

as in *Carpodaptes*. Enlarged medial incisor anteriorly inclined, long, slender. Alveolus of I_2 indicating very reduced, peglike tooth. Canine and P_3 tiny, single-rooted, crowns buttonlike; crown of C with slight anterior overhanging projection. P_4 bladelike, very high crowned, relatively very large (almost twice as long as M_1); apex considerably higher than any other tooth; enamel of buccal side extending downward much below enamel of any other tooth, and relatively lower than in *Carpodaptes*. 8 to 9 apical cusps closely spaced, varying in expression from tiny and sharp to nearly indistinguishable traces; talonid merging with main blade, height equaling that of trigonid of M_1 ; latter forming continuation of P_4 blade. Trigonid of M_1 with paraconid situated directly anterior to protoconid, both cusps equally prominent. M_{2-3} slightly larger than in other two genera, sometimes with incipient mesoconid.

At least 3 teeth present anterior to P^2 . P^2 reduced, single-rooted, with one main cusp, as in *Carpodaptes*. P^{3-4} polycuspsate, greatly enlarged, noticeably larger than molars; cuspule development as in *Carpodaptes*, but teeth larger, relatively longer; P^3 larger than P^4 , with variable anteroexternal extension ("spur"). Upper molars larger but otherwise similar to those of *Carpodaptes*. Mandible deeper than in other two genera.

Discussion: *Carpolestes* is well represented by more than 80 specimens, many of them unusually complete. All of the lower teeth except I_2 are known, and many more upper dentitions of this genus are preserved than of the other two combined. One specimen (PU 17978) includes the root or alveolus of each of three teeth anterior to P^2 , presumed to have been two incisors and a canine (see p. 37).

Two nearly complete palates (PU Nos. 17709, 19422) of *Carpolestes dubius* reveal the presence of palatal vacuities. They may have been characteristic of all carpolestids, but no palatal evidence is available for the other two genera. There are no palatal vacuities in *Plesiadapis*.

Szalay (1972b) proposed that *Carpolestes* be regarded as a junior synonym of *Carpodaptes* on the premise that the number of apical cusps of P_4 might not be a valid generic criterion. From the descriptions and discussions presented above, it is clear that this criterion (and others) are real distinctions separating the late Paleocene carpolestids into two groups which deserve generic rank. As noted above, *Carpolestes* is more specialized in several features than *Carpodaptes*.

Carpolestes nigridentis Simpson, 1928

Figures 23, 27A, 27B

Carpolestes nigridentis Simpson, 1928: 7.*Litotherium complicatum* Simpson, 1929: 10.*Carpolestes aquilae* Simpson, 1929: 10.Holotype: AMNH 22159, right mandible with P_1 - M_2 .Holotype of *L. complicatum*: AMNH 22196, left P^3 .Holotype of *C. aquilae*: AMNH 22233, right mandible with P_1 - M_3 .

Hypodigm: Types and AMNH Nos. 22187-22190, CM Nos. 11518, 11524, 11549, 11557, 11665, 11702, and PU No. 20718, from Bear Creek; PU Nos. 17978, 19543, from "Clark Fork" beds, Bighorn Basin; and YPM Nos. 24614 and 24615, from Paint Creek.

Horizon and Locality: latest Paleocene ("Clarkforkian") of Montana and Wyoming and earliest Eocene (Wasatchian) of Wyoming: Eagle Coal Mine, Beer Creek, Montana (Fort Union Formation); Paint Creek Locality and other sites in the Bighorn Basin, northwestern Wyoming (Polecat Bench Formation).

Emended Diagnosis: P^3 differing from that of *C. dubius* in having 5 prominent buccal cusps, with anterior one fully as developed as others, resulting in noticeably more elongate anteroexternal "spur" (projection); anterior 2 cusps slightly separated from posterior 3.

Discussion: Simpson (1929: 10) diagnosed *C. aquilae* as follows: "Length P_4 - M_2 , 6.2 mm. P_4 about 10% smaller than in *C. nigridens* and slightly smaller relative to the molars. Molars relatively narrower basally." It is now almost certain that the features cited by Simpson are typical of individual (intraspecific) variation, and that there are no characters (within the known, limited fossil evidence) that consistently separate these two species. They are therefore synonymized.

Only one P^3 (AMNH 22196) has been recovered from Bear Creek, the locality of the type mandible, but it is undoubtedly from the same species. Examination of all known specimens of *Carpolestes* reveals no consistent differences in size or morphology between *C. nigridens* and *C. dubius* except in the form of P^3 (Figs. 27, 28). AMNH 22196 has five distinct buccal cusps, the anterior two forming a pronounced antero-lateral projection. Consequently, the length of the buccal side of the tooth is nearly twice that of the lingual side. Three other specimens (PU 17978, 19543, YPM 24614) reveal a P^3 of similar form and are here referred to *C. nigridens*. Although some variation in the morphology of P^3 does occur in *C. dubius*, no individual shows such a pronounced anteroexternal spur as in *C. nigridens*.

It may be significant that all the specimens here allocated to *C. nigridens* come

from sites generally regarded as later "Clarkforkian" or Wasatchian in age, while those that can be definitely referred to *C. dubius* are from the earliest "Clarkforkian" Princeton Quarry level (Silver Coulee beds). Since the one diagnostic feature of *C. nigridens* is a further specialization of P^3 over that of *C. dubius*, it would be expected to occur stratigraphically higher.

PU 17978 contains, in addition to P^3 , the root of P^2 , an alveolus for the canine (?), and roots of two more anterior teeth, interpreted as incisors. Unfortunately the maxillary-premaxillary suture is indiscernible, due to poor preservation. The root of the lateral incisor is round in cross section and smaller than that of the medial incisor; it is about the size of the root of P^2 . The root of the medial incisor is elliptical in cross section and oriented obliquely to the other anterior teeth, indicating that it is probably the most anterior tooth. The front of the specimen is crushed, but there is some indication that the left premaxilla has been superimposed onto the right incisor region, thus strengthening the supposition that the medial incisor is indeed the most anterior tooth. The crowns of the upper incisors are not preserved. Szalay (1972b: fig. 1-9) recently referred an upper (?) incisor from Bear Creek tentatively to *C. nigridens*. Although it is superficially similar to that of archaic primates such as *Plesiadapis*, the incisor is probably referable to the plagiomenid *Planetetherium* (Rose, 1973); consequently, the crowns of the upper incisors of carpolestids remain unknown.

Carpolestes dubius Jepsen, 1930
Figures 5C, 24, 25, 27C, 27D,
29-31, 34E, 34F

Carpolestes dubius Jepsen, 1930: 520.

Holotype: PU 13275, right mandible with C , P_4 - M_2 , roots of I_1 and P_3 , alveolus of I_2 .

Hypodigm: Type and PU Nos. 13276, 13305 (Jepsen's "allotype"), 14069, 14077, 14235,



Figure 23. *Carpolestes nigridentis* Simpson, holotype, AMNH 22159, right dentary with P_4 – M_2 . Crown view (above) and lateral view (below). $\times 6$.

14341-14347, 17646, 17647, 17707-17710, 17856-17861, 17926, 17927, 17963, 19013, 19018, 19023, 19030, 19031, 19064, 19080, 19081, 19095, 19109, 19349, 19385, 19406, 19409, 19422, 19436, 19849, 19886, 21548, 21549; MCZ Nos. 19435-19438; all from Princeton Quarry level.

Horizon and Locality: latest Paleocene ("Clark-forkian"), Polecat Bench Formation of Wyoming: Bighorn Basin, including Princeton Quarry, Schaff Quarry, Fritz Quarry, and other nearby sites of approximately equivalent stratigraphic level.

Emended Diagnosis: P³ with four prominent buccal cusps, anterior one slightly separated from three succeeding cusps; incipient fifth cusp at anteroexternal edge; anteroexternal projection much less elongate than in *C. nigridentis*.

Discussion: As noted above, the only recognizable, consistent difference between this species and *C. nigridentis* is in the morphology of P³ (Figs. 27, 28). The incipient anterior buccal cusp arises from a faint anteroexternal cingulum in some individuals. It is this cusp which enlarges in *C. nigridentis* to produce the anteroexternal "spur."

Jepsen (1930) presented a detailed description of *C. dubius* and outlined its distinctions from *C. nigridentis*. The features he listed do differentiate between the type specimens of the two, but when series are examined, it becomes evident that none of the features occur consistently. Particularly variable are the prominence of vertical ridges and development of an internal cingulum on P₄, the height of the trigonid in M₁, and the development of the hypoconulid on M₁ and M₂. The tendency toward merging of the paraconid and metaconid on M₃ (as in the holotype and a few other individuals) seems to occur as a result of anteroposterior compression of the trigonid. However, the trigonid is compressed but otherwise normal in other individuals, so this is not a specific feature either. The dental formula accepted here (see diagnosis of *Carpolestes*) differs from Jepsen's interpretation (see discussion under *Elphidotarsius*,

tarsius, cf. *E. florencae*). Jepsen (1930:521) presumed that P² was two-rooted, but more complete material now available shows this to be a diminutive one-rooted tooth. He noted five cusps in the buccal row of P³. As mentioned above, the most anterior of these is usually a small, incipient cusp; it is never as prominent as the other four cusps. This is the most important distinction between *C. dubius* and *C. nigridentis*; and, in fact, Jepsen did point out that in P³ of *C. dubius*, the anteroexternal projection is noticeably smaller than in the type of "*Litotherium complicatum*" (= *C. nigridentis*).

Like the large sample of *Carpodaptes hazelae*, the sample now available for *Carpolestes dubius* offers an exceptional opportunity to observe the extent and kind of intraspecific variability which may occur in adult carpolestids. The population is essentially homogeneous in age; only adults are known (based on complete eruption of M₃, and absence of specimens preserving identified deciduous or erupting teeth), and very few could be considered senescent. As in other species of carpolestids, there are only minor variations in the molars, which, except for M₁, differ little even interspecifically throughout the family. The specialized premolars, P₄ and P³⁻⁴, display much more variability.

Only one specimen (PU 14235) preserves the enlarged medial incisor (Figs. 5C, 24). It is similar to that in *Carpodaptes* in being more slender (laterally compressed) and longer than in *Elphidotarsius*. In *Carpolestes* the incisor is nearly twice as long from base to tip as in *Elphidotarsius*. Unlike *Elphidotarsius*, it does not broaden at the base of the crown, but is nearly as narrow (mesiodistally) there as at the tip. The ridge which formed the lateral (distal) border of the dorsal face of the incisor in *Elphidotarsius* has migrated mesially in *Carpolestes* to occupy a more central position on the dorsal aspect of the tooth. As a result, what was the dorsal face in *Elphidotarsius* now inclines sharply toward



Figure 24. Above: *Carpolestes dubius* Jepsen, PU 14235, left dentary with medial incisor, M_{1-2} , crown view. $\times 6$. Below: *Carpolestes dubius* Jepsen, PU 19409, left dentary with C- M_3 , medial view. $\times 6$.

the midline in *Carpolestes*. At the base of the crown, the ridge meets a weakly-developed internal cingulum. The incisor is curved in two planes: dorsally at the tip of the crown (more so than in *Elphidotarsius*), and toward the midline at the tip.

There are no evident wear facets on this incisor.

A few specimens preserve the reduced anterior teeth (I_2 , C, P_3) which are all small, peglike, and single-rooted, as in *Carpodaptes hobackensis*. I_2 is often dis-

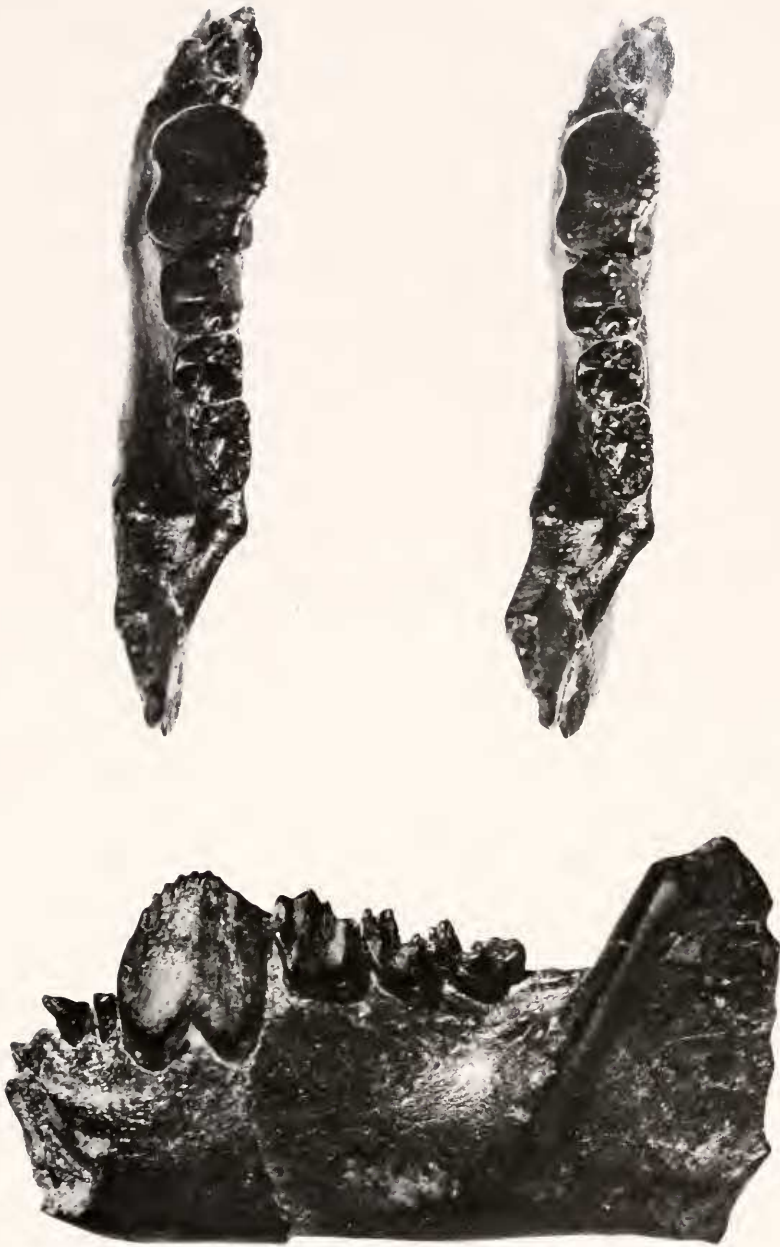


Figure 25. *Carpolestes dubius* Jepsen, PU 19409, left dentary with C-M₃. Crown view (above), lateral view (below). Schaff Quarry. $\times 6$.

placed buccally (as deduced from the alveolus) in relation to the other anterior teeth (PU Nos. 17860, 19409). The enamel of the crown of the canine overhangs an-

teriorly but in P₃ this tendency is reduced (PU 17857) or lacking (PU 19409).

P₄ shows the greatest range of variation of any of the teeth. Size varies considerably

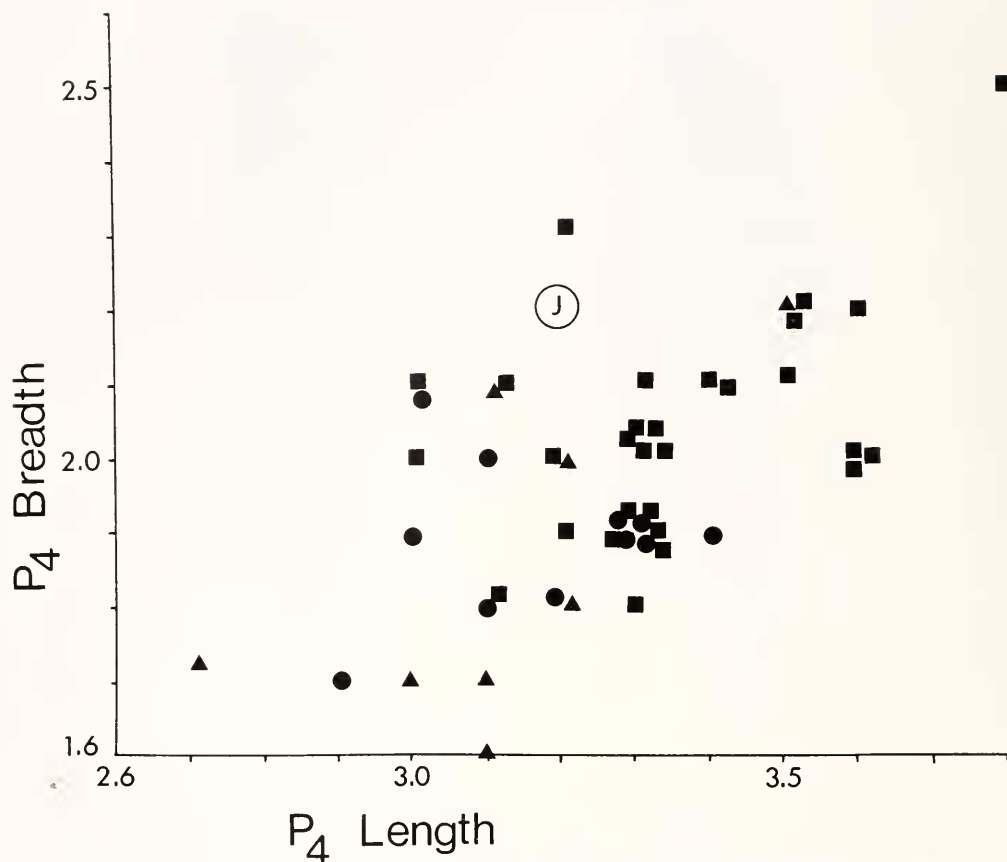


Figure 26. Scatter diagram of P_4 dimensions of *Carpolestes*. Black squares = *C. dubius*. Black circles = *C. nigridens*. Black triangles = *Carpolestes* sp. Circled J = *Carpodaptes jepseni*, holotype.

(see table). The apical cuspules may be sharp and distinct (PU Nos. 19409, 21549) or rather indistinct (holotype); their definition does not appear to be necessarily a function of the degree of wear. They are followed by a talonid cusp which smoothly continues the blade. There are usually eight apical cuspules, the eighth separated somewhat from the preceding seven and only slightly higher than the most anterior one. Some individuals show a faint indication of a ninth cuspule just anterior to the talonid (MCZ 19437). On the other hand, only seven apical cusps are present in PU 21549. The homologies of the apical cusps are not at all obvious, as they were in

Elphidotarsius, but it is likely that proliferation of apical cuspules has occurred primarily at the front of P_4 (i.e., the original trigonid cusps are now situated at the end of the apical cusp sequence). A vertical ridge is present beneath each apical cusp on the lingual side. These ridges vary in distinction but are usually correlated with the degree of definition of the apical cusps. The ridge beneath the eighth cusp is always faint since this part of the tooth is concave, forming a posterointernal depression. This excavation is always present but is variable in depth. As noted above, the sinuous shape of the crest of P_4 (viewed occlusally) is due in part to this depression.

Vertical ridges may be present buccally as well, but are always much less distinct. Crown height of P_4 is variable, and like cusp definition, does not appear to be necessarily correlated with age or wear. P_4 - M_3 are exodaenodont (see above, p. 11), particularly the buccal side of P_4 . The enamel above the anterior root of P_4 extends lower than that above the posterior root in some individuals (PU 19409) a condition more pronounced lingually than buccally in PU 19886. In others (e.g. PU 19030) the enamel over the posterior root descends lower. The development of an internal cingulum on P_4 is variable. Some specimens, such as the holotype, have no internal cingulum (as noted by Jepsen, 1930). Jepsen apparently regarded the absence of an internal cingulum as a specific feature of *C. dubius*, but his paratype, PU 13284, has a weakly-expressed internal cingulum. It should be noted, however, that PU 13284 is recorded as coming from upper "Clark-forkian" beds, so it may represent *C. nigridens*. Other specimens that are undoubtedly associated with upper teeth referable to *C. dubius* have a basal cingulum extending across the entire lingual surface (PU Nos. 19031, 21549, MCZ 19438). The internal cingulum, when present, is usually better developed on the posterior half of the tooth (PU 17710, 19385). It may be developed anteriorly and posteriorly, but less so or not at all in the middle of the tooth (PU 17860). P_4 varies also in shape at the base of the crown (viewed occlusally). The shape is roughly quadrate but slightly laterally constricted at the midsection (between the roots). In some specimens, the posterior half of the tooth is more laterally compressed than the anterior half (PU 19409); in others the anterior half is more compressed (PU 17861). Some specimens of P_4 are relatively quite narrow buccolingually (PU 17861). These features have been cited to illustrate the exceptional variability of P_4 in *C. dubius*. Although most other samples of carpolestid species are considerably smaller, it appears that similar

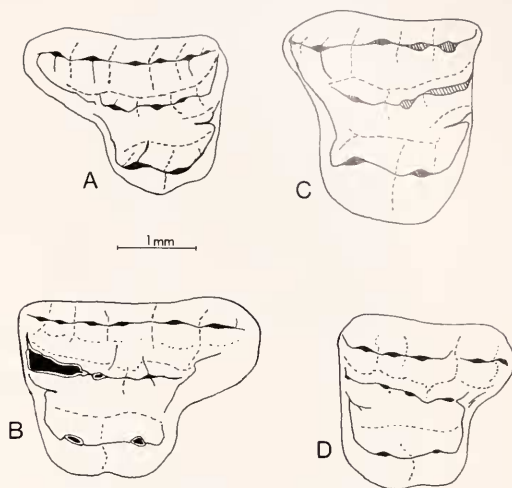


Figure 27. Comparison of P^3 in *Carpolestes*, to same scale. *C. nigridens*: A) PU 19543, left P^3 ; B) YPM 24614, right P^3 . *C. dubius*: C) PU 19349, left P^3 ; D) PU 14077, right P^3 .

variation is typical of carpolestids in general.

The lower molars of *C. dubius* are much less variable than P_4 . Variation in size is not so apparent as in P_4 . A faint external cingulum develops on the molars of some individuals, but it is never very distinct and is often absent. A weak internal cingulum may develop on the trigonid of M_1 (holotype and PU 17710), but this, too, is often absent. The trigonid of M_1 and the talonid of P_4 are invariably the same height. (In PU 19409 [see Figs. 24, 25] the talonid of P_4 appears to be lower than the trigonid of M_1 ; this is due to breakage and subsequent distortion of this specimen.) The posterior edge of P_4 and the anterior edge of M_1 are compacted, forming a continuous blade from the anterior edge of P_4 to the protoconid of M_1 .

At least fifteen specimens of upper dentitions (see Figs. 29, 30, 34F) are referable to *C. dubius*, more than are known in any other carpolestid. The most anterior tooth known is the diminutive P^2 . As aforementioned, Jepsen (1930) thought P^2 was two-rooted, but specimens now known (PU

TABLE 5. METRICAL DATA FOR LOWER CHEEK TEETH OF *CARPOLESTES DUBIUS* FROM PRINCETON QUARRY LEVEL.

		N	OR (mm)	\bar{x}	s	V
P ₄	length	26	3.0–3.6	3.32 ± .03	.172 ± .024	5.2 ± .7
	breadth	27	1.8–2.3	2.01 ± .02	.120 ± .016	6.0 ± .8
M ₁	length	23	1.6–2.0	1.87 ± .02	.105 ± .015	5.6 ± .8
	breadth	23	1.5–2.1	1.67 ± .03	.150 ± .022	9.0 ± 1.3
M ₂	length	15	1.4–1.7	1.54 ± .02	.074 ± .014	4.8 ± .9
	breadth	15	1.4–1.7	1.54 ± .02	.074 ± .014	4.8 ± .9
M ₃	length	6	2.0–2.3	2.13 ± .05	.121 ± .035	5.7 ± 1.6
	breadth	6	1.3–1.4	1.38 ± .02	.041 ± .012	3.0 ± .9
Mandibular depth		7	4.0–5.5	4.87 ± .18	.489 ± .131	10.0 ± 2.7

Nos. 19349, 19422) reveal that it is a one-rooted tooth with one main cusp. A cingulum, faint buccally but well developed lingually, surrounds it; this rises at the anterior and posterior edges of the tooth, posteriorly giving the suggestion of a small second cusp.

Little can be added to Jepsen's (1930: 521–522) accurate and detailed description of P³ and P⁴. Compared to P₄, the morphol-

ogy of P³ and P⁴ is relatively constant. Jepsen described P³ as having five cusps in the external row, but as already noted, the first of these is incipient and never approaches the magnitude achieved in *C. nigridentis*. In PU 13305, on which Jepsen based his description, this cusp is larger than in most other specimens. The cusp is represented only by a slight rise of the anteroexternal cingulum in some others

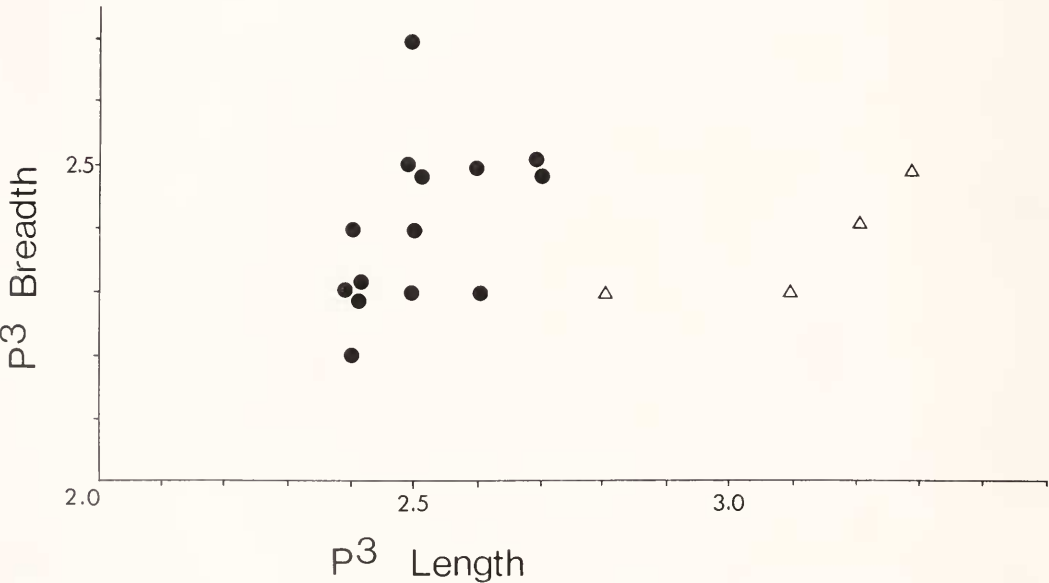


Figure 28. Scatter diagram of P³ dimensions of *Carpolestes*. Black circles = *C. dubius*. Open triangles = *C. nigridentis*.

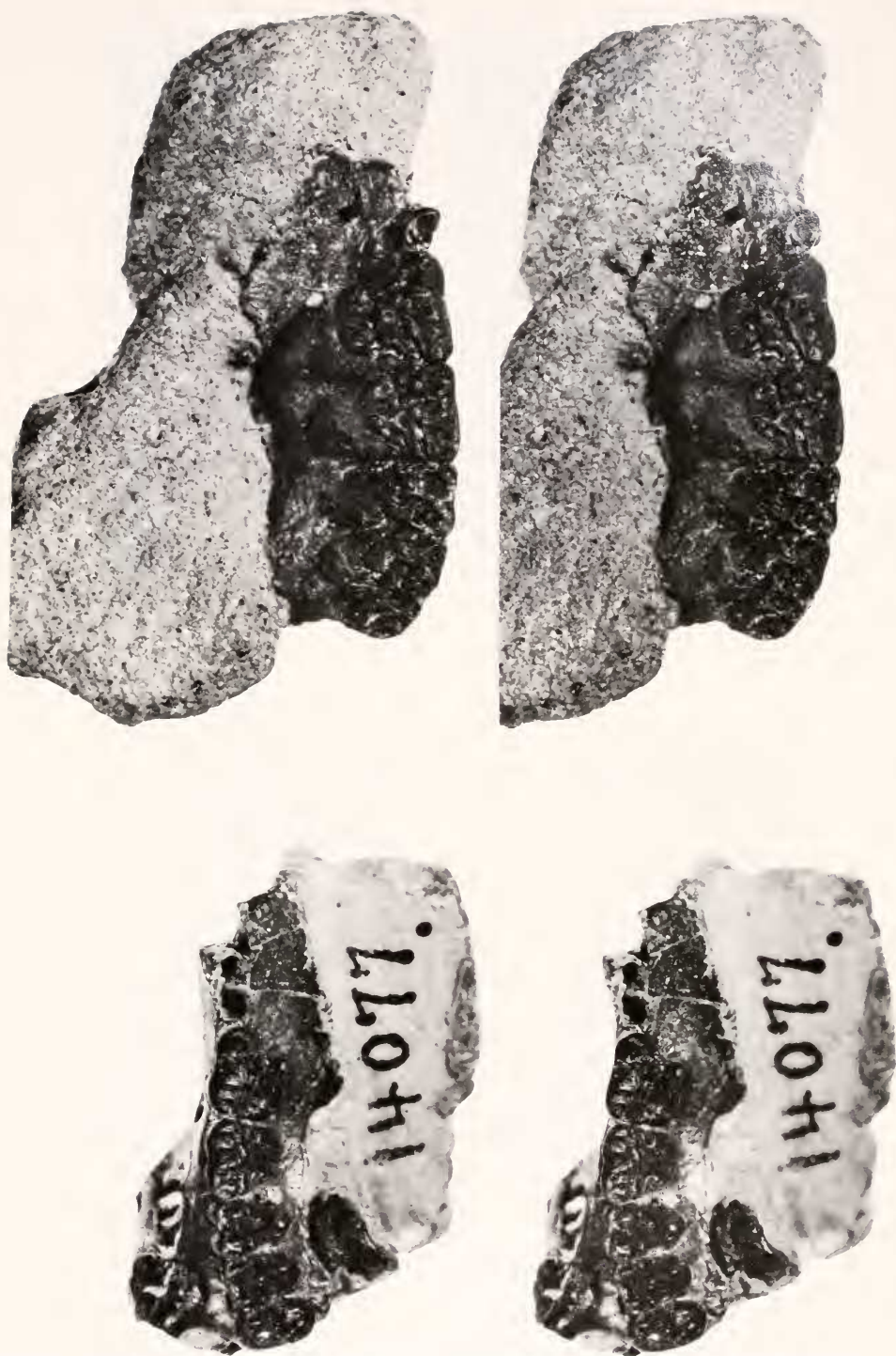


Figure 29. *Carpolestes dubius* Jepsen. Above: PU 19349, left maxilla with P²-M³, crown view. Below: PU 14077, right maxilla with P³-M³, crown view. $\times 6$.

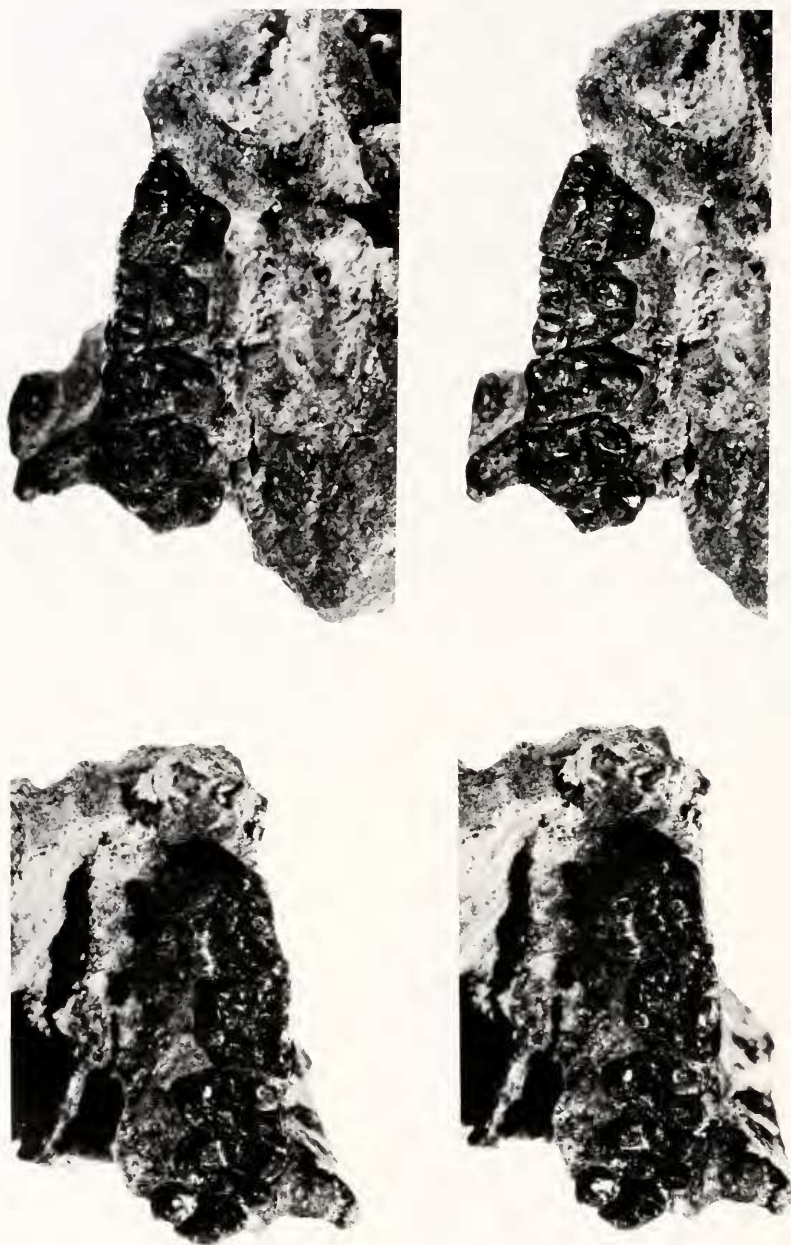


Figure 30. *Carpolestes dubius* Jepsen, PU 17709, palate. Above: right P^3 - M^3 , crown view. $\times 6$. Below: left P^3 - M^3 , crown view. $\times 6$.

(PU 17709, 19439), suggesting that it originated as a stylar cusp. P^1 may show a small sixth cusp at the posterior end of the external cusp row (PU 17709). The

cusps of the medial row in both P^3 and P^4 are difficult to distinguish; this row in both teeth is more of a "rugose crest", as noted by Jepsen. In P^3 the anterior part of this

TABLE 6. METRICAL DATA FOR UPPER CHEEK TEETH OF *CARPOLESTES DUBIUS* FROM PRINCETON QUARRY LEVEL.

		N	OR (mm)	\bar{x}	s	V
P ³	length	14	2.4–2.7	2.51 ± .03	.107 ± .020	4.3 ± .8
	breadth	14	2.2–2.7	2.41 ± .04	.133 ± .025	5.5 ± 1.0
P ⁴	length	12	2.0–2.4	2.23 ± .03	.087 ± .018	3.9 ± .8
	breadth	13	1.9–2.5	2.17 ± .04	.144 ± .028	6.6 ± 1.3
M ¹	length	9	1.5–1.8	1.58 ± .03	.097 ± .023	6.2 ± 1.5
	breadth	9	2.1–2.5	2.27 ± .05	.158 ± .037	7.0 ± 1.6
M ²	length	8	1.4–1.5	1.49 ± .01	.035 ± .009	2.4 ± .6
	breadth	8	2.0–2.3	2.19 ± .05	.136 ± .034	6.2 ± 1.6
M ³	length	6	1.3–1.4	1.32 ± .02	.041 ± .012	3.1 ± .9
	breadth	6	1.9–2.2	2.02 ± .04	.098 ± .028	4.9 ± 1.4

crest bears a distinct, well-developed cusp, and wear patterns suggest the presence of perhaps three additional cusps on this crest (PU 19349). In P⁴ the only recognizable cusp on the medial crest is approximately at the center of the crest. A faint external cingulum may develop posteriorly on P⁴. The enamel of both P³ and P⁴ is crenulated, particularly on the buccal side of each tooth and on the lingual faces of the external and medial cusp rows. P³ is always larger—both broader and longer—than P⁴.

A strong external cingulum is present on the molars. Styler cusps are extremely faint, if present at all. An incipient parastyle is present in several specimens, and a small mesostyle can be detected on M¹ of PU 19349. Anterior and posterior cingula are usually present but less developed than the external cingulum. A faint internal cingulum may unite the anterior and posterior cingula (PU 17709). The hypocone, originating from the posterior cingulum, is usually well expressed, although decreasing in size posteriorly. The anterior cingulum in some individuals (PU 19349) gives rise to a vague, incipient pericone (referred to by Jepsen [1930: 522] as an ectocone); this is rarely detectable except on M¹.

One specimen (PU 19422, a snout with most of the palatal dentition, see Fig. 31) bears an anomalous small right M¹ (left

M¹ is normal). The anomalous tooth is much narrower buccolingually than the other molars, its paracone and metacone aligning with the conules of M² and M³. It lacks a hypocone. The paraconule is well developed, but the metaconule is indistinct. This morphology is strikingly similar to that of dP⁴ of *Plesiadapis* (Simpson, 1935a: 6). The presence in PU 19422 of the fully erupted, complete adult dentition, including right and left P³, P⁴, and M³, seems to preclude any possibility that this represents a deciduous tooth, however.

When *Carpolestes dubius* was described, PU 13305 was the only known maxillary fragment. Although several more specimens are now available, only a few add to our knowledge of palatal and skull anatomy. A partially crushed snout (PU 19422, see Figs. 31 and 32) reveals several details, but much of the structure remains vague as a result of post mortem distortion and the exceptionally hard matrix. The features discussed below are based primarily on this specimen, supplemented by evidence provided from PU Nos. 17709 (a partial palate), 13305, 14077, and 17927.

The maxillae contribute significantly to the face, apparently relatively more so than in *Plesiadapis*. A large infraorbital foramen opens above the posterior root of P³, or more often slightly posterior to that point. As noted by Jepsen (1930), the jugal process

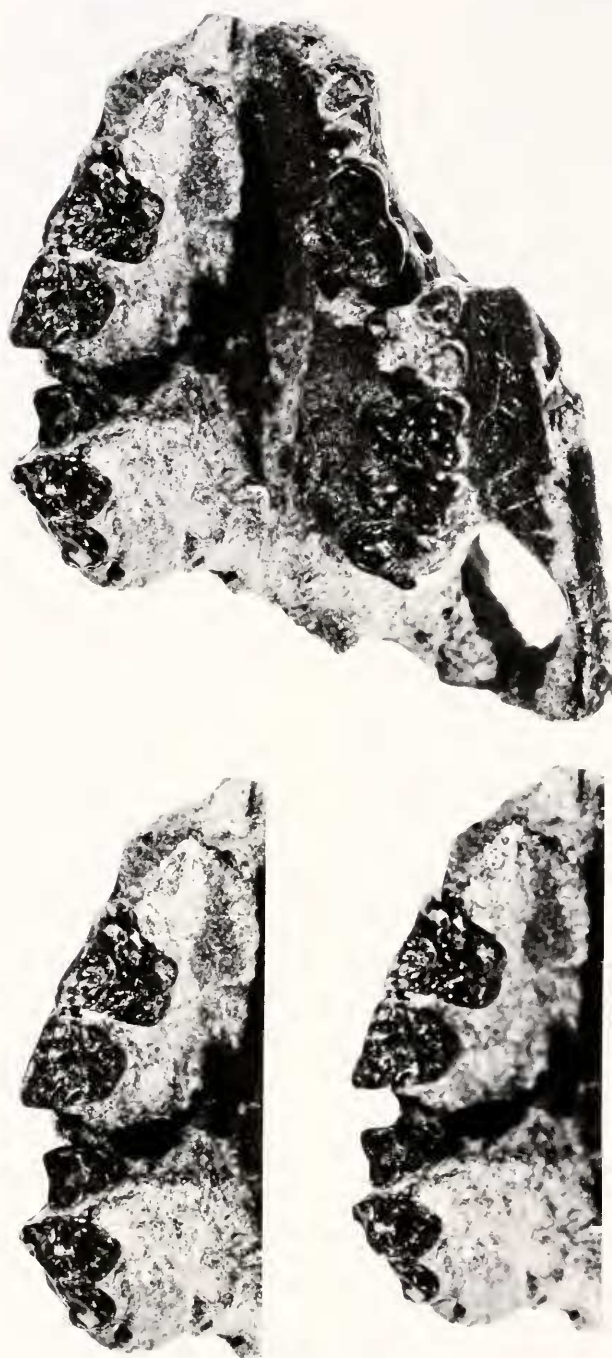


Figure 31. *Carpolestes dubius* Jepsen, PU 19422, snout. Left: palatal view. Right: crown view, right maxillary dentition including P³⁻⁴ and anomalous M¹. $\times 6$.

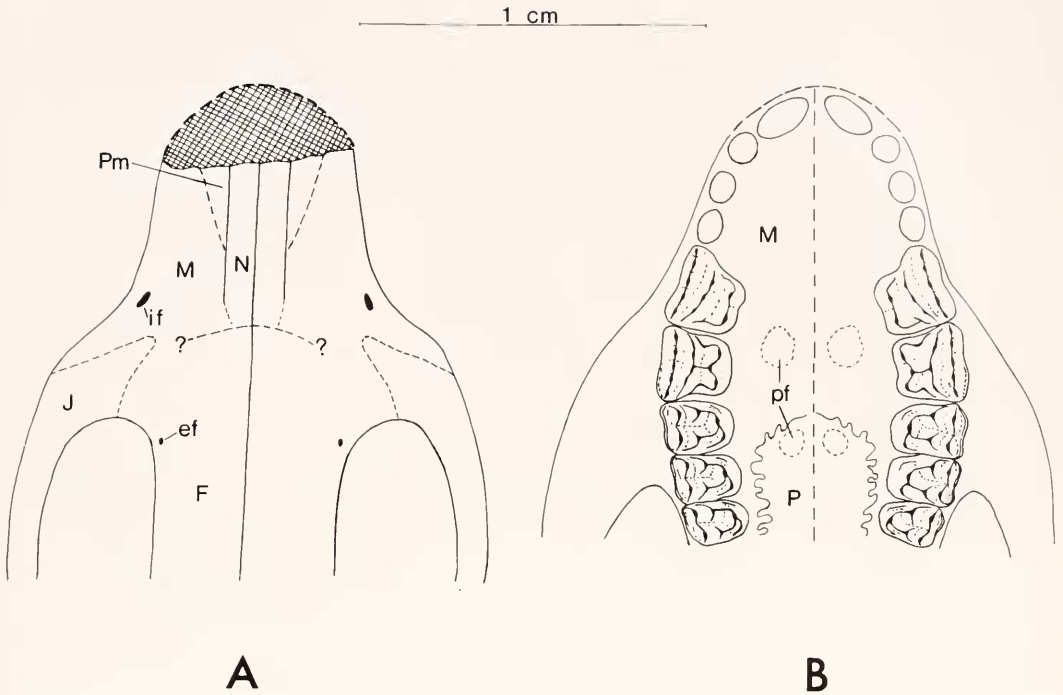


Figure 32. Tentative reconstructions of A) snout, and B) palate of *Carpolestes*, based primarily on PU Nos. 19422, 17709, 17978, and 13305. ef = emissary foramen. F = frontal. if = infraorbital foramen. J = jugal. M = maxilla. N = nasal. P = palatine. pf = palatal fenestrae. Pm = premaxilla.

of the maxilla emerges approximately above M^2 . The jugal portion of the zygomatic arch is preserved in PU 19422 and is robust, as in *Plesiadapis*. The suture between the maxilla and the jugal is nearly horizontal (but slightly more dorsal anteriorly) and extends approximately from above M^2 to above the anterior part of P^1 . Matrix obscures the extent of the lacrimal. The premaxillae, missing anteriorly in PU 19422, are relatively small, contrasting markedly with *Plesiadapis* (Russell, 1959, 1964), where they are very large and form a major part of the snout. A small (emissary?) foramen is present anterolaterally in each frontal, near but just outside the orbital margin.

Jepsen (1930) has noted the peculiar palatal fenestrae in this species. The new material collected since his description unfortunately does not reveal more precisely the position or extent of these fenestrae.

Their occurrence in carpolestids is unique among primates, and their function is unclear. One pair was situated approximately internal to P^3 , bounded at least laterally by the maxillae. There is some indication of a more posterior pair which may or may not have been connected with the anterior pair. These are internal to M^1 or M^2 and appear to be within the palatine; they may possibly be enlarged posterior palatine foramina.

The specimens here referred to *C. dubius* are all from Princeton Quarry and nearby sites of equivalent stratigraphic level, and only specimens from this earliest "Clark-forkian" horizon are included in the hypodigm. All referred lower dentitions are from localities at which they are associated with maxillary dentitions containing P^3 diagnostic of *C. dubius*. P^3 with *C. nigridens* morphology has not been found at this horizon. Separation of the two species

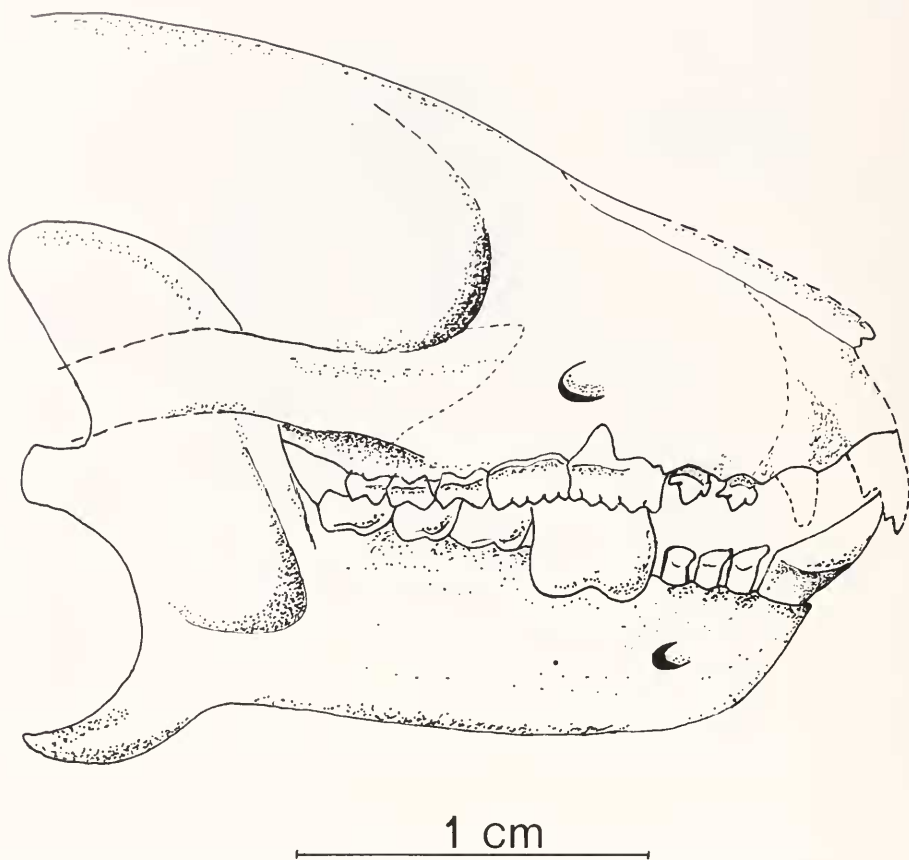


Figure 33. Tentative reconstruction of the skull of *Carpolestes*, based on PU Nos. 14235, 19409, 19422, 14077, 17978, and 19349. Angular process of mandible restored from PU 21399 (*Carpodaptes hazelae*); upper canine restored from AMNH 33980 (*Carpodaptes hazelae*).

on stratigraphic criteria eventually may prove justifiable, but is precarious at present.

C. dubius is surely the immediate ancestor of *C. nigridentis*. Future discoveries may reveal that P^3 morphology is variable and not taxonomically significant, and that *C. dubius* should be placed in synonymy. As long as the two species are maintained, however, mandibular dentitions of *Carpolestes* will be assignable to species only if associated with P^3 . Consequently, about a dozen specimens, including those from Buckman Hollow (USNM 21280) and Togwotee Pass (AMNH 88198), and several from the Big Horn Basin, must, for the

present, be referred to *Carpolestes*, species indeterminate.

A tentative reconstruction of the skull of *Carpolestes*, based primarily on specimens of *C. dubius*, is presented in Figure 33.

The Phyletic Position of *Saxonella*

D. E. Russell (1964) described *Saxonella crepaturae*, from the Middle Paleocene of Walbeck, Germany, and referred it to the Carpolestidae. Differences between the new form and the North American carpolestids compelled Russell to propose two subfamilies, the Carpolestinae, for the North American genera, and the Saxonel-

linae, for the new genus. Like the North American forms, *Saxonella* has a "plagiaulacoid" dental complex in the mandible, but the premolar specialization is not the same as in carpoolestids. In *Saxonella*, P_3 is enlarged and trenchant and P_4 relatively small. Such a difference is fundamental and precludes the possibility of very close relationship between *Saxonella* and carpoolestids. Furthermore, the mandibular dental formula, 1.0.2.3, is reduced beyond that in even the most advanced carpoolestids, although *Saxonella* appears to have been contemporary with the earliest known North American species of the family.

Russell's assignment of *Saxonella* to the Carpoolestidae was, nevertheless, accepted by some authors (e.g., Romer, 1966; McKenna, 1967).

Some features (e.g., molar and incisor morphology, form of P_4 , and mandibular dental formula) are equally or more suggestive of plesiadapid affinities, although the dental reduction in *Saxonella* exceeds even that in contemporary plesiadapids. Moreover, Russell was surely correct in suggesting that other early primates had upper incisors of comparable structure. Van Valen (1969) formally transferred *Saxonella* from the Carpoolestidae to the Plesiadapidae, a view followed by Szalay (1970, 1972b), Simons (1972), and Butler (1973).

The morphology of *Saxonella* points to affinities with both carpoolestids and plesiadapids, but its specializations are comparable in magnitude, although different from, those of either family. Accordingly, *Saxonella* should be separated from both at the family level, as the Saxonellidae, but grouped with them in the superfamily Plesiadapoidea.

MORPHOLOGY AND FUNCTION

The "Plagiaulacoid" Dentition

The lower dentition in carpoolestids is characterized by a hypertrophied, trenchant P_4 , an enlarged medial incisor, and reduced dentition between these, a pattern termed

"plagiaulacoid" (Abel, 1931; Simpson, 1933) in allusion to its occurrence in members of the multituberculate suborder Plagiaulacoidea. The complex is present in several other mammalian groups, including ptilodontoid multituberculates, caenolestoid marsupials (Simpson, 1933; Paula Couto, 1952), phalangeroid marsupials, and the plesiadapoid *Saxonella*. Simpson (1933) concluded that plagiaulacoidy was acquired independently at least four times: probably once in multituberculates, twice or more in marsupials, and once in primates (*Saxonella* then being unknown). The differing homologies of the sectorial tooth in *Saxonella* and carpoolestids make it virtually certain that two independent origins occurred in primates.

The bladelike specialization in these mammals may involve more than one tooth, as in plagiaulacids such as *Ctenacodon*, but is usually restricted to one. In the latter case it is not always the same tooth: in *Saxonella* it is P_3 , not P_4 as in carpoolestids; in caenolestoids it is P_3 or M_1 , and in Australian marsupials it is P_3 (the last premolar). In ptilodontid multituberculates the blade has generally been assumed to be P_4 , but there is some evidence to suggest that it is actually the first molar (Bohlin, 1945; Sloan, Kielan-Jaworowska, personal communication).

The adaptive significance of the "plagiaulacoid" dentition may be generally similar in the varied types possessing it, but dissimilar upper dentitions in most of these mammals suggest that the function is variable. Simpson (1933) concluded that it is an adaptation for herbivory, especially efficient for dealing with coarse vegetation.

The only extant mammals with the "plagiaulacoid" dentition are certain macropodid marsupials (e.g., *Hypsiprymnodon*, *Dorcopsis*, *Aepyprymnus*, *Bettongia*) and the phalangerid *Burrhamys*, Australian forms in which the sectorial lower tooth is opposed by a similar trenchant tooth in the upper jaw. This complex is quite different from that in carpoolestids, and inferences of

carpolestid dental function or diet by analogy with these "plagiaulacoid" marsupials are probably poorly founded. Furthermore, although most of these marsupials feed on vegetation such as fruits, berries, and leaves, at least one form (*Hypsiprymnodon*) is known to ingest substantial quantities of insects and worms (Walker et al., 1968). Simpson (1933) contrasted the unusual upper premolars of *Carpolestes* with the upper teeth of other "plagiaulacoid" mammals and speculated that carpolestids may have been more frugivorous than extant "plagiaulacoid" marsupials.

The upper premolars of some ptilodont multituberculates show superficial similarities to those of advanced carpolestids, but there are indications that multituberculate dentitions functioned differently than those of carpolestids. Almost certainly the sectorial lower tooth of multituberculates was more directly involved with powerful shearing than appears to have been the case in carpolestids.¹ Carpolestids and multituberculates may have been to some extent mutually competitive, but dental resemblances between the two may indicate only that both were specialized herbivores.

The upper teeth of *Saxonella* are less specialized than those of *Carpodaptes* and *Carpolestes*, but not unlike those of *Elphidotarsius*; and it may be postulated that dental function in *Elphidotarsius* and *Saxonella* was similar.

Major Features and Trends in the Carpolestid Dentition and Skull

The lower dental formula is $\overline{2.1.3.3}$ in *Elphidotarsius* and $\overline{2.1.2.3}$ in *Carpodaptes* and *Carpolestes*. *Elphidotarsius* has many

similarities to the contemporary plesiadapid *Pronothodectes*, but its P_4 , enlarged and bladelike, is characteristically carpolestid. It retains three lower premolars, like *Pronothodectes*. P_2 , judging from its alveolus, was a small, single-rooted, peglike tooth. P_3 is small relative to P_4 but is comparatively unreduced and premolari-form. In *Carpodaptes* and *Carpolestes*, the mandibular dentition is similar to that of *Elphidotarsius*, but further specialization and hypertrophy of P_4 has resulted in the loss of P_2 and the simplification of P_3 into a single-rooted peg.

Upper dentitions of carpolestids (Fig. 34), as for many other fossil mammals, are much less well represented in collections than are mandibles. Upper teeth or partial dentitions are known for *Elphidotarsius* cf. *florencae*, *Carpodaptes hazelae*, *C. cygneus*, *Carpolestes nigridens*, and *C. dubius*, the latter species being the best known. The most anterior upper teeth are unknown in *Elphidotarsius* and *Carpodaptes*. Specimens of *Carpolestes* suggest an upper dental formula of $\overline{2.1.3.3}$ in this genus. The maxillary-premaxillary suture is poorly preserved and unclear in all specimens preserving this region, but its apparent position is consistent with the interpretation of the dental formula given here.

A number of features of carpolestids observed to be more fully developed in the later, more specialized species may be regarded as trends. For example, size tends to increase through time. *Carpodaptes* is generally larger than *Elphidotarsius*, and *Carpolestes* is always larger than all but one of the species (*Carpodaptes jepseni*) of the other two genera. While this trend involves primarily the cheek teeth, P_4 and P_3 - P_4 are particularly affected. Some exceptions have already been noted: *Carpodaptes hobackensis* and *C. cygneus* are smaller than the known species of *Elphidotarsius* and may be representative of a side branch of the genus which was decreasing in size; *Carpodaptes jepseni* is fully as large as *Carpolestes*. Correlated with the gradual

¹ Hahn (1971) illustrated teeth of the Upper Jurassic paulchoffatiid multituberculates that demonstrate that their premolars were not involved in shearing; they show considerable abrasive wear and erosion at the apices of the cusps, somewhat as in carpolestid premolars (see below).

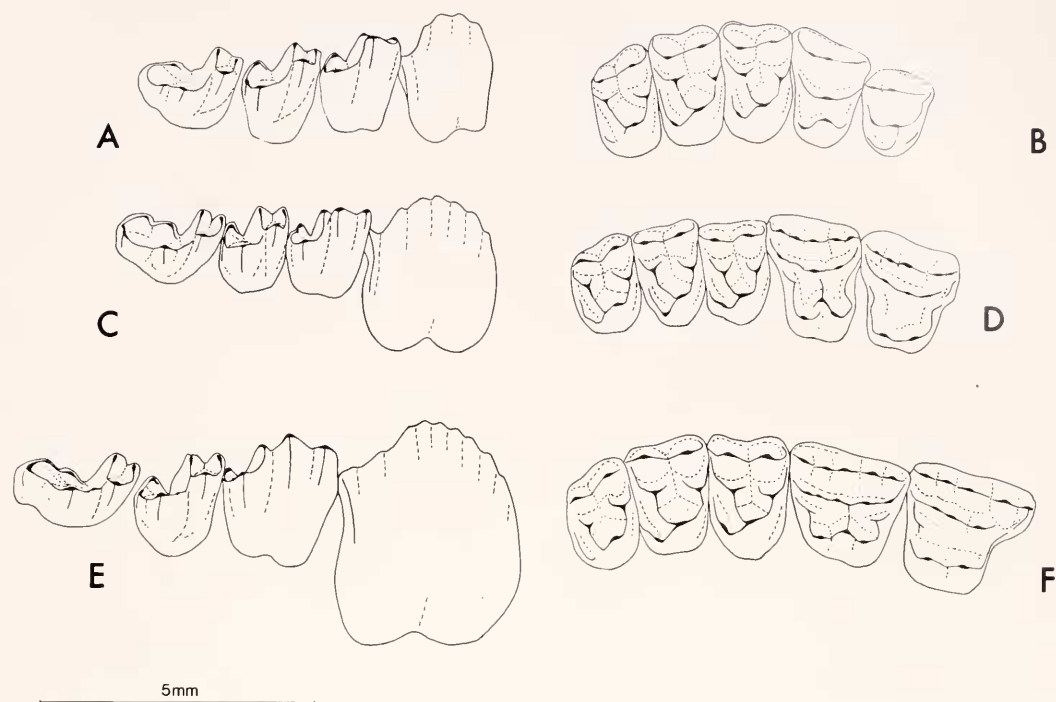


Figure 34. Lower cheek teeth (P_4 – M_3) and upper cheek teeth (P^3 – M^3) of carpolestids, to same scale. A and B) *Elphidotarsius* (based on *E.*, cf. *E. florencae*). C and D) *Carpodaptus* (based on *C. hazelae*). E and F) *Carpolestes* (based on *C. dubius*).

increase in size of the teeth is increasing mandibular depth to accommodate the lengthening roots, particularly of P_4 . The mandible of *Elphidotarsius* is relatively shallow (2.8–3.5 mm); that of *Carpodaptus* is somewhat deeper (3.1–4.0 mm; 5.5 mm in *C. jepseni*); and the jaw of *Carpolestes* is comparatively deep (4.0–5.5 mm). There is also a trend toward lengthening and slenderizing the enlarged medial incisor.

Associated with size increase is the increasing specialization of P_4 and P^{3-4} (see Fig. 34). The enlargement and specialization of these teeth occurred, at least in part, at the expense of the anterior teeth (except the medial incisors), which underwent reduction through time. Specialization was accomplished by the addition of accessory cusps, with the result that in the two more specialized genera cusp homologies are not entirely clear. As in

most Paleocene primates, the antemolar modifications are more diagnostic than are the molars, which remain relatively conservative (paromomyids such as *Phenacolemus* and *Micromomys* [Szalay, 1973] have an enlarged P_4 , reduced anterior teeth except the incisor, and relatively conservative molars).

Specialization of P_4 in carpolestids was accompanied by elongation of the trigonid of M_1 . The trigonid cusps of M_1 in *Elphidotarsius* are arranged in a triangle, but in *Carpodaptus* and *Carpolestes* the paraconid and protoconid are drawn out, nearly or exactly in line, and colinear with the cusps of P_4 . The lengthening of the trigonid of M_1 occurs at the expense of the length of the talonid and is relatively more marked in *Carpolestes* than in *Carpodaptus*.

M_3 tends to enlarge in the sequence *Elphidotarsius*–*Carpodaptus*–*Carpolestes*, par-

ticularly by elongation of the third lobe. The hypoconulid of M_3 is typically twinned, and there is often a small mesoconid on the cristid obliqua in later forms. Breadth of P_4 and of the lower molars shows a tendency to increase through time, but this feature is among the most variable intraspecifically and hence of little taxonomic value.

The clearest trend in the upper dentition, as noted above, is toward specialization and hypertrophy of P^{3-4} (associated with the enlargement of P_4). In *Elphidotarsius*, these teeth are smaller than the molars (or P_4 may be about the size of the molars), but in *Carpodaptes* and *Carpolestes* they are noticeably larger than the molars. P^3 changes the most. It is a small, relatively generalized, premolariform tooth in *Elphidotarsius*. In *Carpodaptes* it is already subequal to P^4 , while in *Carpolestes* it is always larger than P^4 and may display a conspicuous anteroexternal projection. P^4 is somewhat specialized in *Elphidotarsius*, already at this stage longitudinally tripartite. These three sections are much more complex in *Carpodaptes* and *Carpolestes*. The latter two genera have a closely similar P^4 , the main distinction being the greater anteroposterior length in *Carpolestes*. Both P^3 and P^4 in the two later genera are polycusate, with numerous accessory cusps.

Intraspecific variability of the teeth has been discussed in the systematics section. The much larger samples of carpolestids now available provide a reasonably adequate basis for concluding, as did Butler (1963: 1), that "paleontologists have tended to underestimate the variability of fossil species."

It should be noted that all known specimens of carpolestids, as far as can be determined, represent adult individuals. In no specimen is there evidence of deciduous or erupting teeth, and those preserving the posterior part of the jaw always reveal a fully erupted M_3 (or its alveolus). Only

a small number of individuals are in advanced stages of wear.

The most conspicuous trend in mandibular morphology is increasing depth, associated with the lengthening of the roots of P_4 . The mental foramen is variable in position beneath P_2 or P_3 in *Elphidotarsius* and below \bar{C} or P_3 in *Carpodaptes* and *Carpolestes*. As in most prosimians, the symphysis was unfused in carpolestids. The posterior part of the mandible is preserved in near entirety only in a few specimens of *Carpodaptes hazelae* (PU 20615, 21341, 21399; see Fig. 35). It is closely comparable to the back of the dentary in *Plesiadapis* (PU 21246). The coronoid process is high and broad. The angular process is recurved and tapers posteriorly, forming a hooklike process much like the angle in other archaic primates such as *Plesiadapis* and *Phenacolemur*, and in such Recent insectivorans as *Ptilocercus*, *Setifer*, and *Neotetracus*. It serves as a point of insertion for the internal pterygoid and part of the masseter. The condyle in *Carpodaptes*, as in *Plesiadapis*, is situated about midway between the angular process and the top of the coronoid, about even with or just slightly above the tooth row. In *Phenacolemur* (PU 21405) the condyle is markedly higher than the tooth row. (This feature, together with dental morphology, suggests that *Phenacolemur* may have been more strictly herbivorous than either *Plesiadapis* or the carpolestids.) The articular surface of the condyle, well preserved in only one specimen (PU 21399), covers the entire dorsal and posterior surfaces of the condyle; its transverse diameter is approximately 1.6 mm.

The few known details about the palate and front of the skull are based primarily on specimens of *Carpolestes dubius* and have been discussed under that species in the section on systematics. Skulls of archaic primates are poorly known. Only that of *Plesiadapis* is reasonably well preserved (Russell, 1959, 1964). *Phenacolemur* (Simpson, 1955; Szalay, 1972a) and *Palaechthon*

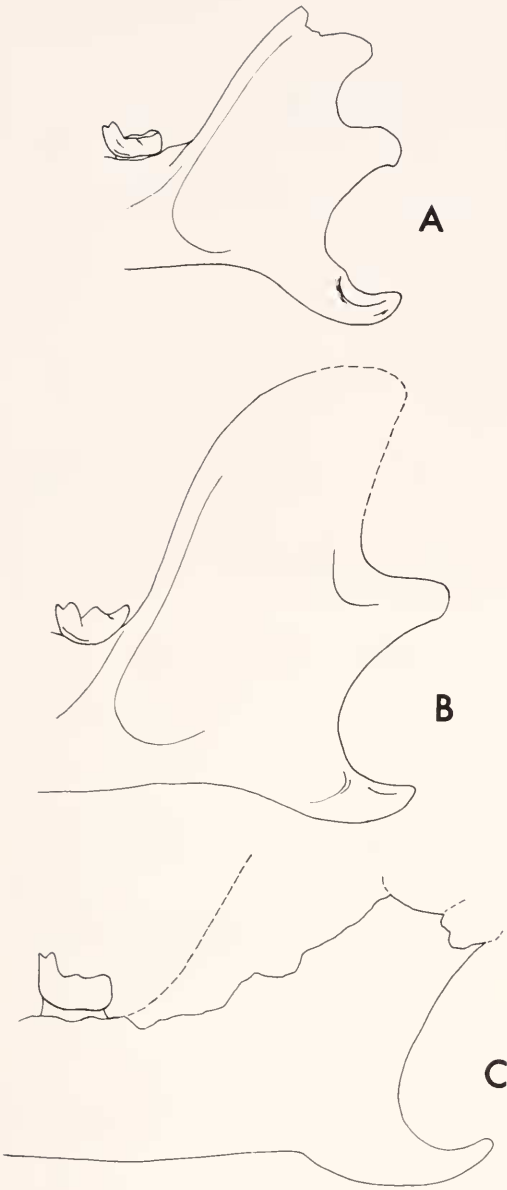


Figure 35. Lateral view of posterior of mandible, not to same scale. A) *Carpodectes hazelae*, PU 21399. B) *Plesiadapis rex*, PU 21246 (reversed). C) *Phenacolemur* sp., PU 21405 (M_3 restored).

(Wilson and Szalay, 1972) are each known from one poorly preserved skull. Present evidence permits few comparisons between *Carpolestes* and these genera, but it is prob-

ably valid to conclude that the palatal (and preorbital) length was relatively much less in *Carpolestes* than in *Plesiadapis*, and was comparable to or slightly less than in *Palaechthon*.

Occlusion and Dental Function

Introduction. Recent cineradiographic studies of living mammals have provided much information on the movement of the mandible and the function of the teeth during feeding (e.g. Ardran et al., 1958; Crompton and Hiiemäe, 1970; Hiiemäe and Ardran, 1968; Hiiemäe and Crompton, 1971; Hiiemäe and Kay, 1972, 1973; Kay and Hiiemäe, 1974a, b; Ride, 1959). For example, it has been established that in the opossum, *Didelphis*, feeding involves four steps: ingestion, transfer of food to the molar region, mastication, and deglutition, sometimes including regurgitation for further preparation by the teeth (Hiiemäe and Crompton, 1971). Mastication, the step involving preparation of the food by the cheek teeth, can be separated into three components: the upstroke or preparatory stroke, the power stroke (occlusal or near occlusal stroke), and the downstroke or recovery stroke (Hiiemäe, 1967; Hiiemäe and Ardran, 1968; Crompton and Hiiemäe, 1969a, 1970; Hiiemäe and Crompton, 1971; Kay and Hiiemäe, 1974a, b).

Two stages of mastication have been observed. The first, a puncture-crushing stage involving no direct contact of the upper and lower teeth causes wear on the tips of the cusps, resulting eventually in exposure of the dentine through windows in the enamel. The term "abrasion" has been used to describe wear resulting from the puncture-crushing stage of mastication (Hiiemäe and Kay, 1973; Kay and Hiiemäe, 1974a). Gingerich observed striated wear facets on the posterior surface of the metacone and anterior surface of the protoconid in *Adapis* (Gingerich, 1972) and on the front of the main cusp of P_4 in *Phenacolemur* (Gingerich, 1974a). He believes this wear to be a result of "orthal retrac-

tion", which took place during the puncture-crushing stage.

The second stage of mastication is direct tooth-to-tooth occlusion during which shearing, crushing, and often grinding¹ occurs (Crompton and Hiiemäe, 1970; Kay and Hiiemäe, 1974a). This results in striated wear facets on the crests which join the cusps of the teeth, and in the basins. The resulting wear has been called "attrition" (Kay and Hiiemäe, 1974b). A number of recent investigations have made use of these facets in interpretations of the function of molariform teeth in therian mammals (e.g., Butler, 1952, 1972, 1973; Crompton, 1971; Crompton and Hiiemäe, 1969a, b, 1970; Gingerich, 1972, and in press; Hiiemäe and Kay, 1973; Kay and Hiiemäe, 1974b; Mills, 1955, 1966, 1967).

The power stroke of the occlusal stage of mastication in primates has two components, each forming a set of matching occlusal wear facets on the upper and lower teeth. Mills (1955, 1967) has used the terms "buccal phase" and "lingual phase" to describe the movement of the mandible during the power stroke, and the resultant wear facets. According to him, the buccal phase on the active side coincides with the lingual phase on the opposite side, promoting balanced occlusion (and simultaneously formed buccal and lingual phase facets). Hiiemäe and Kay (1972, 1973; and Kay and Hiiemäe, 1974b), on the other hand, have shown convincingly that no such balanced occlusion occurs in the primates they studied cinefluorographically. Wear facets thus reflect successive phases of the power stroke on the same side of the jaw. Because buccal phase and lingual phase, as defined by Mills (1955), differ from observed mandibular movements and methods of formation of wear facets, Hiiemäe and Kay (1972) have proposed the terms "Phase I" and "Phase II" to describe the successive phases of the power stroke. During Phase I

in primates, the active side of the mandible moves upward, medially, and slightly anteriorly, until the teeth are in centric occlusion. The facets produced face buccally on the lower teeth, lingually on the uppers. In Phase II, the active side moves downward and further medially and anteriorly (in such forms as *Ptilocercus* and *Erinaceus* the jaws moves posteromedially, rather than anteromedially, during Phase II [Mills, 1967]). Phase II facets face lingually on the lower teeth, buccally on the uppers. This phase involves a slight shift in direction from that of Phase I, which is reflected in a difference in the direction of Phase I and Phase II facets. However, wear facets with striations intermediate in direction between those of Phase I and Phase II have been observed in *Plesiadapis*, suggesting that the two phases in this form were parts of a single, transverse movement (Gingerich, in press).

Carpolestids. Phase I and Phase II facets have been observed on upper and lower molars of carpolestids and are mapped in Figures 36–38. Facets have been numbered according to the scheme introduced by Crompton (1971) and followed by Gingerich (in press) and Kay and Hiiemäe (1974a). Facets 1–7 are formed during Phase I, facets 9 and 10 during Phase II. Occluding wear surfaces on upper and lower teeth are given the same number. Molar function in all three genera of carpolestids was very similar to that in *Plesiadapis* (Gingerich, in press). Discussion of the relative tooth movements involved in forming each facet have been detailed by Kay and Hiiemäe (1974a) and Gingerich (in press).

Orthal retraction facets have not been detected in carpolestids.

Lower Teeth (Figs. 36, 37). All seven Phase I facets occur on one or more of the molars of each genus. Facets 1 and 5, on the posterior surface of the trigonid, differ markedly in size on the different molars. An oblique ridge (formed by the contact of the cristid oblique with the protocristid)

¹ Precise definitions of these three terms are presented by Kay and Hiiemäe (1974a).

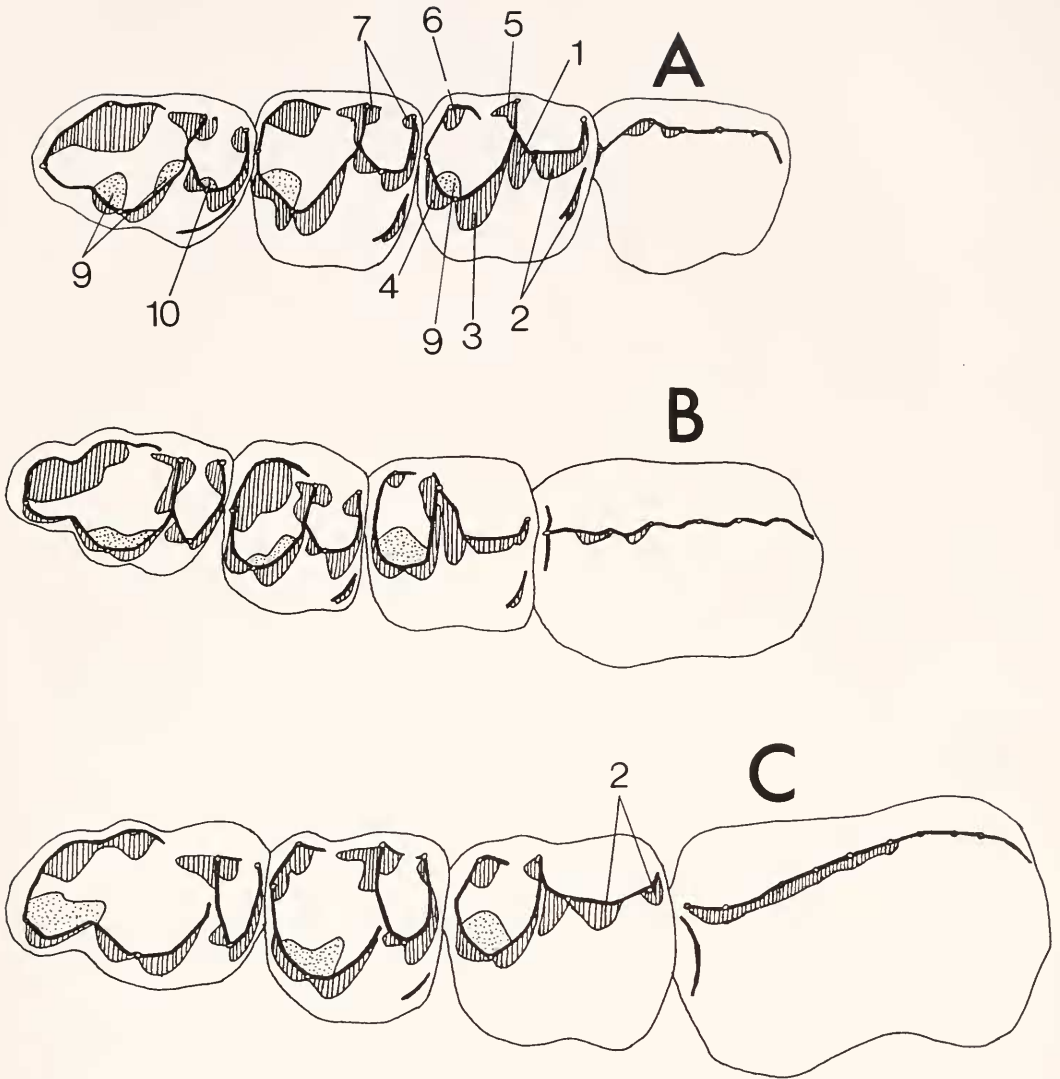


Figure 36. Occlusal wear facets of lower teeth, P_4 - M_3 . Vertical lines denote Phase I facets; stippling denotes Phase II facets. Numbering of facets is after Crompton (1971) and Kay and Hiiemäe (1974b). A) *Elphidotarsius*; B) *Carpodaptes*; C) *Carpolestes*.

demarcates facet 1, on the posterior surface of the protoconid, from facet 5, on the posterior surface of the metaconid. On M_1 , in which the protoconid is the highest cusp, facet 1 is as large as or larger than facet 5, while on M_2 and M_3 , where the metaconid is as high or higher than the protoconid, facet 5 is larger than facet 1. The enlarge-

ment of facet 5 at the expense of facet 1 appears to be typical of many primates. Facet 2 is lengthened on M_1 by virtue of the elongation of the trigonid. In some specimens an additional shearing surface parallel to facet 2 is developed on the anteroexternal cingulum (M_1 or M_2), as in *Plesiadapis* (Gingerich, in press). Facet 6

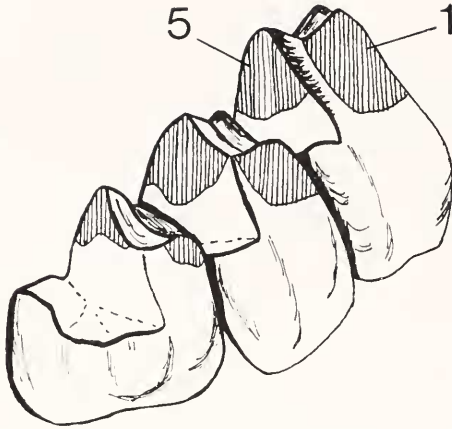


Figure 37. Occlusal wear facets 1 and 5 (Phase I) in *Elphidotarsius* (posterior oblique view of right M_{1-3}).

develops on the buccal surface of the entoconid and may extend to include the hypoconulid region. This facet is most extensive and best developed on M_3 . Facet 7, variably developed on the buccal surface of the paraconid and metaconid, is a continuation of facet 6 of the next anterior tooth (Kay and Hiiemäe, 1974a) and in some cases these two facets appear to be confluent with facet 2 (on the paracristid). Shearing surfaces may be increased in number by fenestration of any Phase I facets; this is, of course, prevalent in individuals at advanced stages of wear.

Shearing facets (Phase I) on P_4 are, surprisingly, poorly developed or absent from most specimens. A few specimens of *Elphidotarsius* reveal small striated facets, probably homologous with facets 1 and 5, on the posterobuccal surface of the two posterior apical cusps (the presumed homologues of the protoconid and metaconid). Specimens of *Carpodaptes*, as a rule, show no better-developed wear surfaces than in *Elphidotarsius*. In *Carpolestes* some individuals have small striated facets on the buccal surface of apical cusps on the posterior two-thirds of the tooth. These small facets become confluent on a few heavily-worn individuals (e.g. PU 19030; see Fig. 39D). A few specimens of P_4 in *Carpolestes* display heavy abrasive wear (Fig. 39). No

P_4 's examined show such extensive Phase I facets as indicated by Butler (1973: fig. 11).

Phase II facets are much less clear than those of Phase I. Facet 9, on the lingual surface of the hypoconid, has been detected on one or more molars of each genus, but facet 10, on the lingual surface of the protoconid, has been observed only on M_3 on a few (e.g. *Elphidotarsius*, PU 14285). This is in accord with Butler's (1973) observation that Phase II facets are best developed on M_3 and less so anteriorly. There are no Phase II facets on P_4 , i.e., there is no wear on the lingual side of P_4 .

Upper Teeth (Fig. 38). Phase I facets 1-7, matching those of the lower molars, are developed on upper molars of all three genera. As in *Palenochtha* (Kay and Hiiemäe, 1974a) and *Plesiadapis* (Gingerich, in press), facets 1-4 are developed on the conule crests as well as on the preparacrista, centrocrista, and postmetacrista; parallel crests are labelled "a" and "b". For example, facet 1a forms on the preparacrista, 1b on the preparaconule crista, parallel to the preparacrista. Facets 1b, 2b, 3b, and 4b are well developed on M^1 and M^2 ; hence the conules are large. On M^3 facet 2b is not developed and the metaconule is small. Facet 5, on the lingual surface of the preprotocrista, is prominent on all three

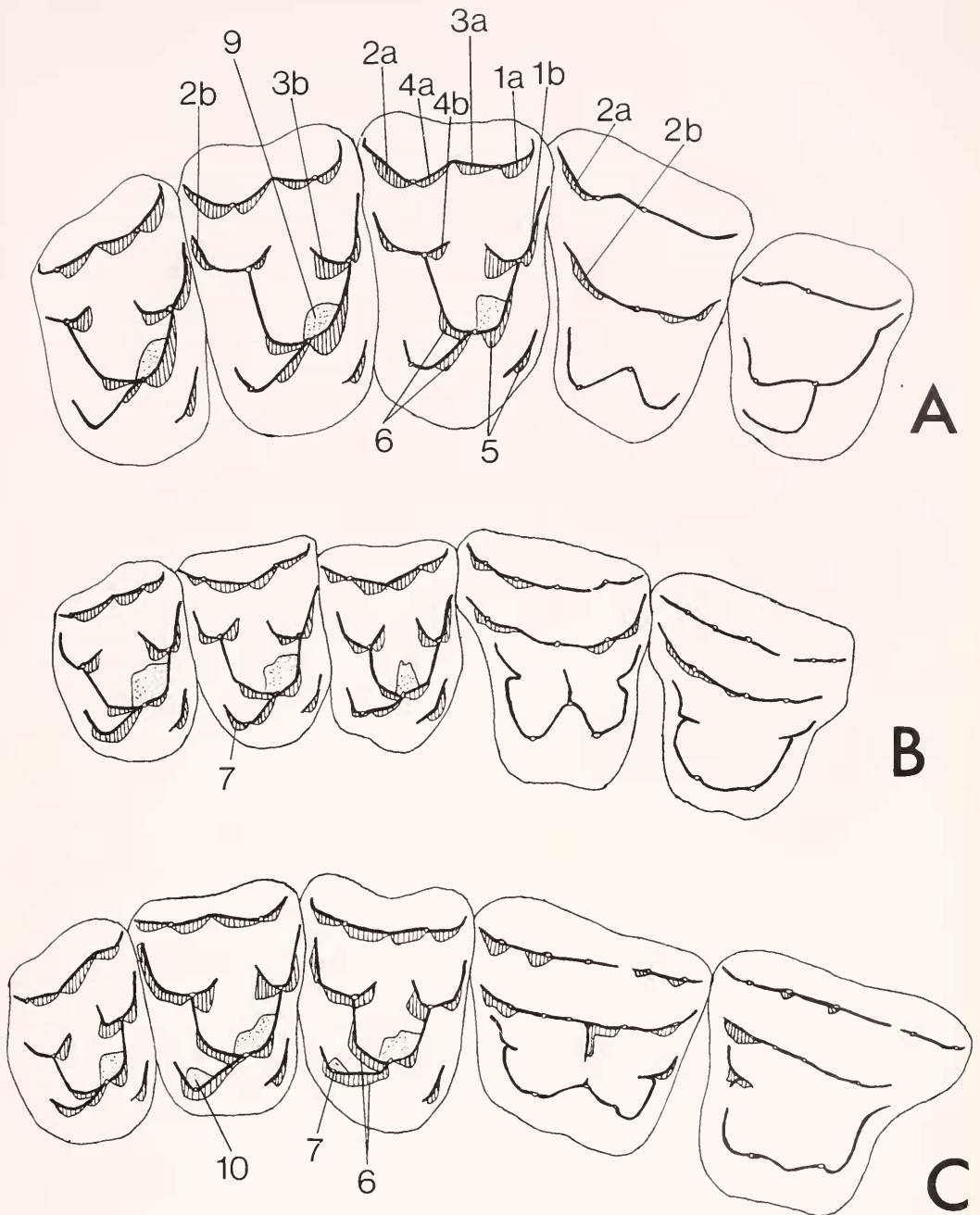


Figure 38. Occlusal wear facets of upper teeth (P^3 – M^3), depicted as in Figure 36. A) *Elphidotarsius*; B) *Carpodaptes*; C) *Carpolestes*.

molars and in *Carpodaptes* and *Carpolestes* extends onto the precingulum in many individuals. Facet 6 forms on the postproto-crista and on the “nannopithec fold” (the

crest joining the protocone and hypocone). It is confluent with facet 7 on the lingual surface of the hypocone. Facet 7 was not detected in *Elphidotarsius*.

As in the lower molars, Phase II facets are less evident than Phase I facets, but facet 9, on the buccal surface of the protocone, is relatively distinct in many specimens. Facet 10, on the buccal side of the hypocone, was observed only in a few individuals of *Carpolestes*.

P^{3-4} are somewhat difficult to interpret, for although numerous specimens are now available, many show little or no wear. Phase I facets are developed on the lingual surfaces of the posterior third of the buccal and central crests on P^4 in all three genera. These match facet 2 on the trigonid of M_1 and are homologous with facets 2a and 2b on the molars. The significant wear on P^3 and P^4 appears to be due to abrasion, causing the tips of the cusps in the buccal and central crests to become blunt and fenestrated (Figs. 39G, H). This type of wear in *Carpodaptes* and *Carpolestes* is particularly evident on the posterior half of P^3 and anterior half of P^4 , i.e., the region which occludes with P_4 . Small striated wear facets form on the flattened periphery of these cavitations in some specimens, and in *Carpolestes* they may extend to the short crests between the central and lingual row of cusps. They are not so large as depicted by Butler (1973: fig. 11), indicating that Phase I wear in P^{3-4} , although present, is of minor importance. No phase II facets have been detected on P^3 or P^4 of any carpolestid.

Interpretation. These observations indicate that the molars of carpolestids functioned very much like those of *Plesiadapis*, but Phase II was evidently less prominent than in the latter genus and seems to have been much less important than Phase I. The molars were the significant teeth involved in shearing (Phase I) and grinding (Phase II); the specialized premolars were less effective during this stage of mastication. Shearing capability in the molars was enhanced by increasing the number of shearing surfaces in the same ways as has been observed in *Palenochtha* and *Plesiadapis*.

One method, called "en echelon" shear (Hiemäe and Kay, 1972), involves the development of successive shearing surfaces (e.g., in upper molars, facets 1a and 1b, or facet 5 on both preprotocrista and precingulum; in lower molars, facet 2 on both paracristid and anteroexternal cingulum; see Figs. 36, 38). Individual shearing surfaces were multiplied by fenestration as in *Plesiadapis* (Gingerich, in press). Grinding, the major function in Phase II, involved all the molars but was more prominent posteriorly, as noted also by Butler (1973).

The function of the peculiar, specialized P_4 and P^{3-4} of carpolestids is of particular interest. My conclusions differ somewhat from those of Butler (1973). Despite its bladelike appearance, P_4 was apparently not used primarily in shearing. Phase I facets observed on a few specimens indicate that such function occurred to a limited extent, but the poor development or absence of these facets on the majority of specimens indicates that P_4 was not very important during Phase I. The absence of Phase II facets indicates that P_4 was insignificant in Phase II function.

The premolars of many mammals are involved chiefly in the preparation of food prior to the masticatory stage involving Phase I and II. This "puncture-crushing" stage results in abrasion. P_4 and P^{3-4} of carpolestids display mainly abrasive wear, which has resulted in erosion of the tips of the cusps and exposure of dentine in heavily worn individuals (Fig. 39). The term "puncture-crushing" seems inappropriate to describe the probable use of these teeth in carpolestids, however. P_4 probably functioned in a sawlike manner, cutting or tearing food which was held partly by the polycusate P^{3-4} . Phase I facets in P^{3-4} , as in P_4 , are poorly developed and often absent, suggesting that Phase I shearing was not the primary function of these teeth. Similarly, the absence of Phase II facets on P^{3-4} indicates that their function was insignificant during this stage of mastication.

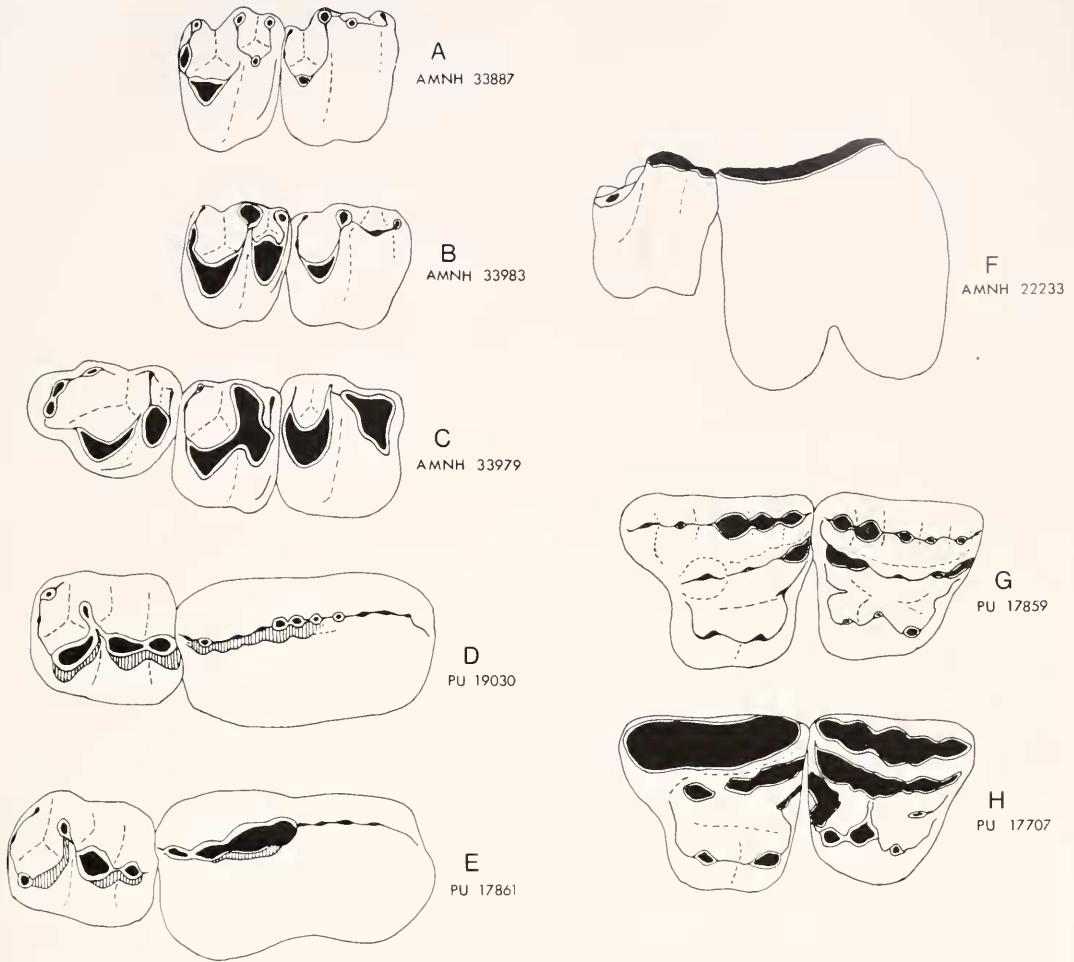


Figure 39. Abrasive wear in carpolestids, exposing dentine (black areas). Vertical lines in D and E are Phase I wear facets. A–C) progressive degrees of wear in *Carpodaptes hazelae*. A and B are right M_{1-2} ; C is right M_{1-3} (crown views). D–H) progressive stages of wear in *Carpolestes*. D and E are right P_4-M_1 of *C. dubius* (crown views); F is right P_4-M_1 of *C. nigridentis* (lateral view); G and H are left P_3-4 of *C. dubius* (crown views).

Dietary Inferences

Even in extant mammals it is often difficult, from dental and mandibular structure, to postulate specific feeding preferences. In extinct forms, which often have no living analogues, inferences regarding diet must be largely speculative. Concerning dietary habits of Paleocene mammals in general, Van Valen and Sloan (1966: 264) have remarked:

“Upon considering the diversity of food habits of recent species with teeth generally similar among the species, we are impressed with the impossibility in the foreseeable future of reconstructing in any detail the diets of Paleocene mammals. When there is a phyletic trend towards a more herbivorously adapted dentition, it is probably valid to say that most of the later members of this clade were herbivorous, or more

herbivorous than their ancestors. There are very few Paleocene mammals of any kind for which a more detailed statement on diet is possible."

While specific food preferences of extinct forms may be impossible to establish, some general comments may nevertheless be offered. As noted above, it is probably invalid to base inferences regarding the diet of carpolestids on extant "plagiaulacoid" marsupials. The functional interpretations discussed above show that carpolestids used their molars much as plesiadapids did. Unfortunately, this provides little precise insight, of course, for the diet of plesiadapids can only be speculative. Carpolestid premolars were probably used primarily during the puncture-crushing stage of mastication, suggesting that the diet of carpolestids may have consisted of herbage, fruits, and seeds tougher than those eaten by *Plesiadapis*. Similarities in morphology and wear patterns between carpolestid molars and those of the Recent *Tarsius*, a predominantly insectivorous primate, further suggest that carpolestids were capable of feeding on insects and may have included them in their diet.

ORIGIN, AFFINITIES, AND INTERRELATIONSHIPS OF CARPOLESTIDS

Simpson (1937a: 8) remarked: "In spite of the extraordinary specialization of the premolars, the facts now known about the carpolestid dentition seem to me to point to the early primates and to no other group." I agree totally with this statement. Some early authors (e.g., Matthew and Granger, 1921; Jepsen, 1930), however, did not recognize carpolestids as definite primates, and some recent students have continued to question their primate status. Saban (1961) listed them as Mammalia, *Incertae sedis*. Martin (1968) and Charles-Dominique and Martin (1970) have suggested that allocation of *Plesiadapis* and its allies to the Primates should be reassessed.

Cartmill (1972) recently advocated the more drastic step of transferring the "archaic prosimians" from the Primates to the Insectivora, an unsatisfactory solution which does not accurately reflect the phylogenetic relationships of these forms. Although the evidence now at hand indicates that some archaic prosimians did not possess the three features that Cartmill selected as diagnostic of Eocene and later primates (postorbital bar, petrosal bulla, and opposable hallux or pollex with nail), the dental evidence points overwhelmingly to primate, not insectivoran, affinities, and it is the dentition that constitutes most of the known evidence of the archaic prosimians. Known Paleocene primates are not generally considered ancestral to later ones, and it is only to be expected that they should have remained primitive in some features that later, and perhaps independently, evolved in the primate stock. If one accepts Cartmill's three features as definitive of the Primates, the only recourse would be to establish a new order for the Paleocene forms. In our present state of knowledge, such a move would be premature. I believe that the mainly Paleocene archaic prosimians are definitely primates and should be grouped in the infraorder Plesiadapiformes (Simons, 1972)¹.

It has long been recognized that carpolestids share numerous features with members of the Plesiadapidae, and comparisons of carpolestids with all other Paleocene primates indicate that the closest affinities are with that family. Simpson (1937b: 162) noted the striking likeness of *Elphidotarsius* to *Pronothodectes*. "M₂₋₃ are almost exactly like those of *Pronothodectes*, so much so that were this form known from those teeth alone it would have to be defined as a species of *Pronothodectes*." He later wrote (Simpson, 1940: 205): "There is a remarkably close resemblance in the lower molars

¹ The suborder Plesiadapoidea Romer, 1966, is rejected here because it was proposed conditionally, and because it is a homonym of the superfamily Plesiadapoidea Trouessart.

between carpolestids and plesiadapids, but it does not extend to all parts of the dentition and may indicate nothing more than that all are early primates." This now seems to be an overly cautious view. There are, in fact, marked similarities of *Elphidotarsius* to *Pronothodectes* extending beyond the lower molars (see Fig. 41). Upper teeth of *Elphidotarsius*, unknown when Simpson wrote, are even closer structurally to those of *Pronothodectes* than are the lowers. The upper molars are virtually indistinguishable (except in size) from those of *Pronothodectes*, and P^3-4 are noticeably similar in both genera. I_2 , \bar{C} , and P_2 are reduced in both forms, and the dental formulae are the same as far as can be determined. These resemblances, and the lack of such close similarity to other archaic primates, argue strongly for community of origin of the two families (as Simpson [1937a] suggested), probably in the Puercan.

Van Valen (1969: 295) proposed that carpolestids evolved "from *Pronothodectes* or just possibly some unknown more primitive plesiadapid." The latter alternative seems more probable, inasmuch as *Pronothodectes* is not known from strata below those which contain *Elphidotarsius*. A new, undescribed, plesiadapoid genus from Purgatory Hill (Sloan, 1969) may shed light on this problem. As demonstrated above, derivation of *Elphidotarsius* from a *Pronothodectes*-like form would not be difficult. Virtually no modification of the molars would be involved, the trigonid of M_1 being only slightly extended in *Elphidotarsius*. P_4 of *Elphidotarsius* may be termed submolariform, the apical cusps homologous to the three trigonid cusps (with the addition of an anterior accessory cuspule), and a talonid cusp behind. P_4 is typically premolariform in *Pronothodectes*. In the Puercan *Purgatorius unio*, it has a distinct paraconid and may show enamel thickenings in the metaconid region (Clemens, 1974). Of the upper premolars, P^4 has three longitudinal crests in both *Elphidotarsius* and *Pronothodectes*. P^3 in

the former, however, is not divided into three longitudinal parts, as in *Pronothodectes* (and later carpolestids). The simpler P^3 , like that of *Elphidotarsius*, was probably the ancestral condition. Carpolestids and plesiadapids should be placed in a superfamily Plesiadapoidea (along with *Saxonella*), to reflect their close relationship.

Intergeneric relationships of carpolestids are easily interpreted. The conclusion reached here is that the three genera are members of a single lineage. All three are found in the same general area and they constitute a morphologic sequence found in successive strata. It is highly probable that *Elphidotarsius* gave rise to *Carpodaptes*, and the latter gave rise to *Carpolestes* (Fig. 40B). No known evidence contradicts this hypothesis.

Some authors (e.g. Schaeffer et al., 1972) advocate a much more complex interpretation of phylogeny, suggesting that taxa that seem to form a direct lineage with regard to morphology and stratigraphy may actually represent only a few members of a much wider radiation. The application of this concept to carpolestid phylogeny might lead to the conclusion that the three genera do not lie in a single lineage (Fig. 40A).

For example, the sympatric occurrence of *Carpodaptes* and *Elphidotarsius* in the Late Torrejonian Shotgun Local Fauna may suggest that there were two carpolestid lineages, one involving only *Elphidotarsius*, the other comprised of *Carpodaptes* and *Carpolestes*. However, *Elphidotarsius* is known also from Torrejonian beds almost surely older than those at Shotgun, which is the earliest occurrence of *Carpodaptes*. The antecedents of *Carpodaptes* must have passed through a stage, structurally like *Elphidotarsius*, that would be considered in that genus as now defined. No features of *Elphidotarsius* now known exclude it from a position ancestral to *Carpodaptes*.

Even closer resemblances between *Carpodaptes* and *Carpolestes* indicate that these genera must lie in an ancestor-descendant line. Simpson (1937b) was of the

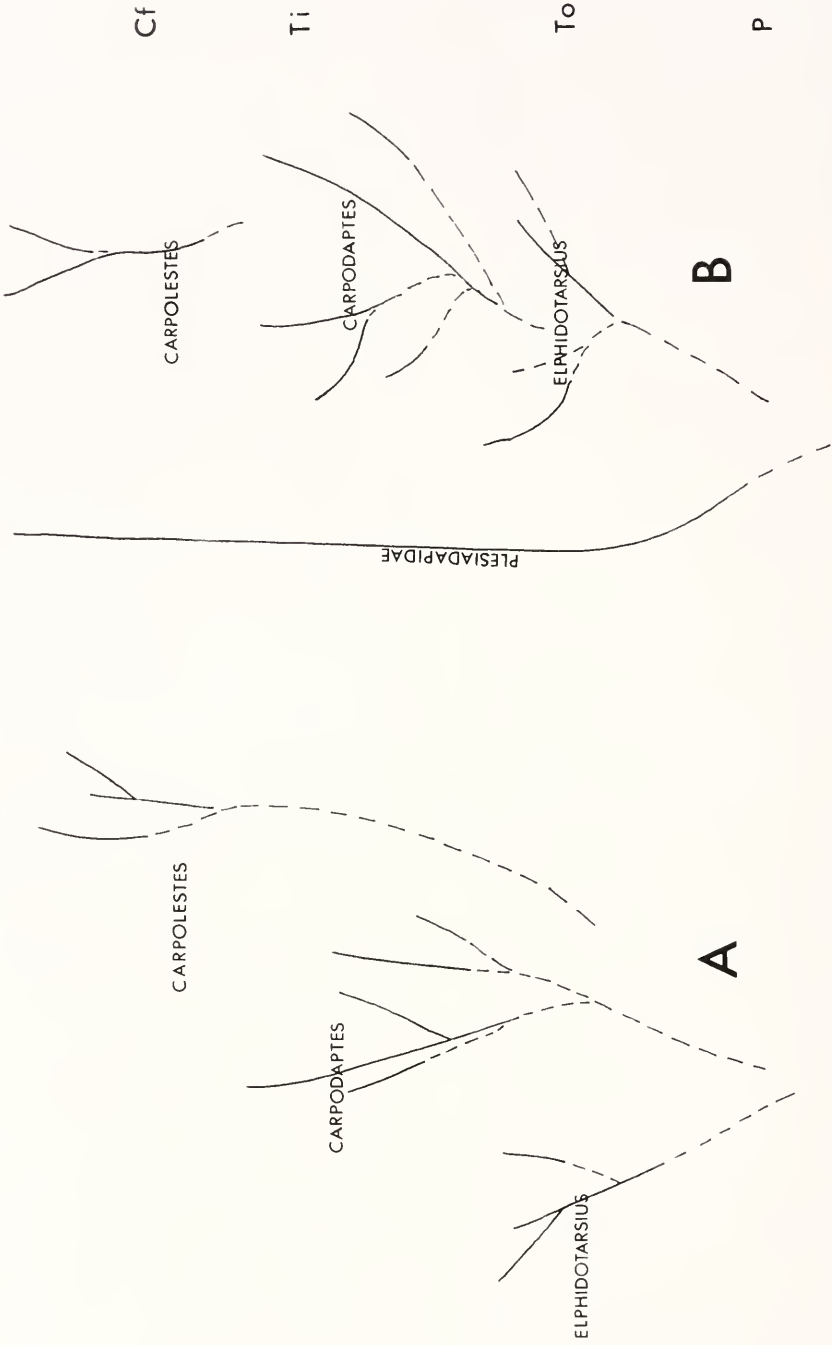


Figure 40. Possible phylogenies of the Carpolestidae (see text).

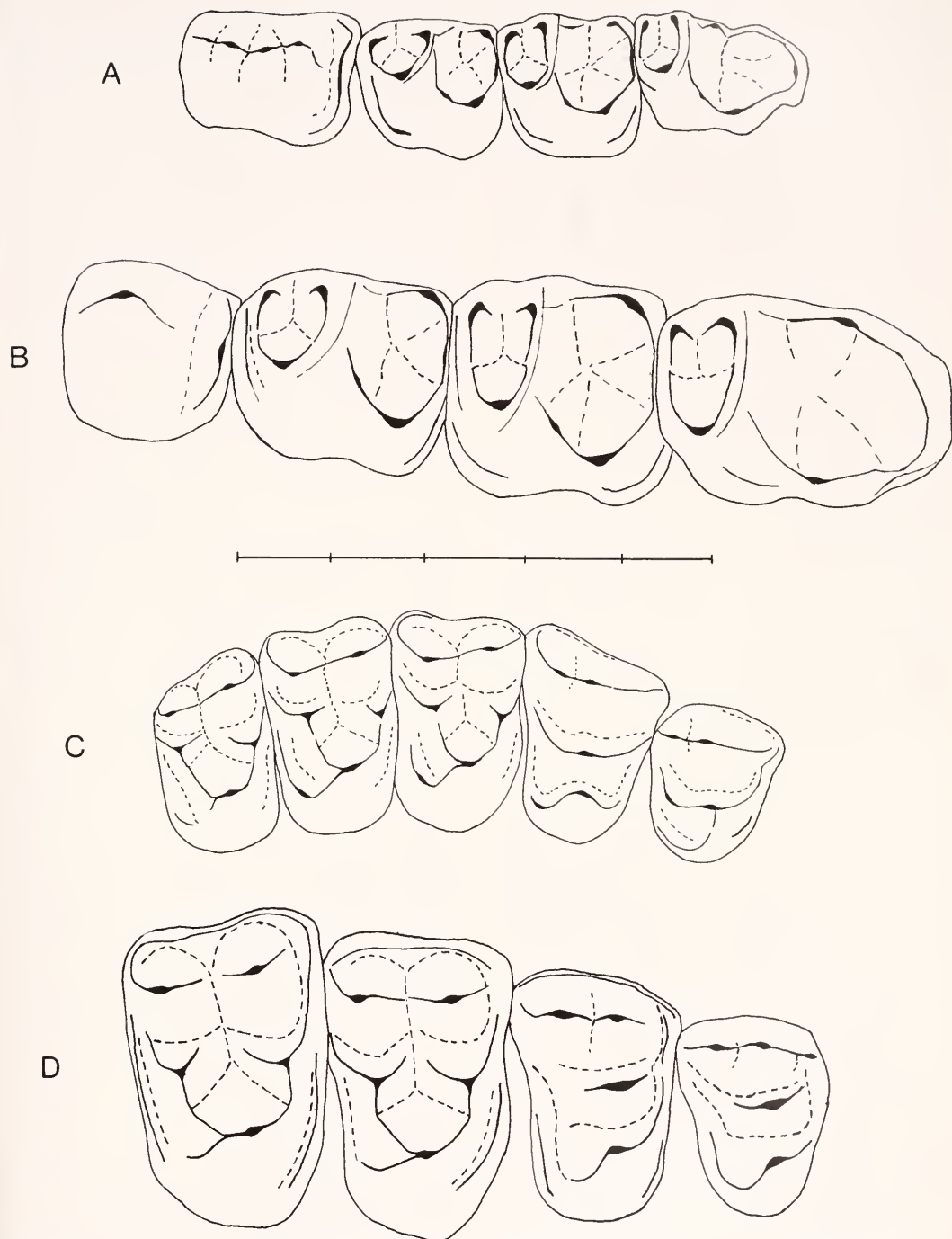


Figure 41. Comparison of *Elphidotarsius* with *Pronothodectes*, to same scale (mm). A) *Elphidotarsius* sp., cf. *E. florencae* Gidley, PU 14282, left P_4 - M_3 . B) *Pronothodectes matthewi* Gidley, AMNH 35462, left P_4 - M_3 . C) *Elphidotarsius* sp., cf. *E. florencae* Gidley, PU 17439, right P_3 - M_3 . D) *Pronothodectes matthewi* Gidley, AMNH 35470, left P^3 - M^2 (reversed).

opinion that these two had evolved in parallel, for he did not believe the age difference between them to be significant. As they are now known, however, all specimens of *Carpodaptes* are invariably from lower strata than those of *Carpolestes*, so Simpson's objection is no longer tenable.

Relationships among carpolestid species are more nebulous. Limited geographic occurrences of most species and our ignorance of precise stratigraphic correlations between many sites make relative age determinations difficult for some species, particularly of the genus *Carpodaptes*. I shall not propose a detailed reconstruction of carpolestid phylogeny, therefore, but some comments may be offered.

Of the two species of *Elphidotarsius*, *E. florencae* is structurally more primitive. *E. shotgunensis* has a longer P_4 and more extended M_1 trigonid, features which place it closer structurally to *Carpodaptes*. However, it is known only as a Late Torrejonian contemporary of *Carpodaptes*, at Shotgun, and unless present at an earlier time, it must be eliminated from consideration as a *Carpodaptes* ancestor.

Relationships among the species of *Carpodaptes* are poorly known. The morphology of *C. aulacodon* provides no immediate clue to its relationships with other species of the genus. The shape of P_4 and configuration and definition of the apical cusps indicate no particularly close relationship to any other species of the genus, nor special proximity to the ancestry of *Carpolestes*.

Carpodaptes hazelae, although the best represented species of the genus, is also difficult to place phylogenetically. Features such as the often well defined apical cusps and the separated talonid cusps of P_4 suggest that this species is not particularly close to the direct ancestry of *Carpolestes*. On the other hand, P^{3-4} are quite similar to those of *Carpolestes*. (It must be emphasized that upper teeth are known in only one other species of *Carpodaptes*.)

Carpodaptes cygneus and *C. hobackensis*

are very closely allied species or, just possibly, variants of the same species. Morphologically, they possess certain features definitely foreshadowing those present in *Carpolestes*: usually poorly defined apical cusps on P_4 , talonid of P_4 not so clearly separated from the P_4 blade, S-shaped conformation of P_4 cusps in crown view, and posterolingual depression in P_4 (*C. hobackensis*). These features led Dorr (1952) to conclude that *C. hobackensis* was probably nearer the direct line of ancestry to *Carpolestes* than either of the other species of *Carpodaptes* then known (*C. aulacodon* and *C. hazelae*). Although this is possible, it must be noted that *C. hobackensis* and *C. cygneus* are the smallest known species of *Carpodaptes* and are, in fact, even smaller than the known species of *Elphidotarsius* in molar dimensions. This may indicate that their particular line of evolution trended toward smaller size, possibly posing an obstacle to their lying in direct ancestry to *Carpolestes*. A hypothetical larger form with morphology like that of *C. hobackensis* would be an ideal ancestor for *Carpolestes*.

Among known species, *Carpodaptes jepsoni* appears to be nearest to the ancestry of *Carpolestes*. In support of this conclusion are the large size, shape of P_4 , and the size of P_4 relative to the molars. The presence of only six relatively well defined apical cusps and a distinct talonid cusp on P_4 are features typical of *Carpodaptes*. If this species is not in or near the ancestry of *Carpolestes*, it must represent a line which closely approached the *Carpolestes* grade of specialization. As with *C. aulacodon*, caution must be exercised in drawing conclusions based on a single specimen.

The two recognized species of *Carpolestes* are unquestionably very closely related. The slightly more specialized P^3 of *C. nigridentis* indicates that this species was a direct derivative of *C. dubius*. This is the only differentiating character discernible in known specimens. Alternatively, the

two may have been representatives of a single polytypic species, but this cannot be substantiated on the basis of present evidence.

ACKNOWLEDGMENTS

I am deeply indebted to Drs. G. L. Jepsen and V. J. Maglio of Princeton University, who granted me the opportunity of studying the extensive collection of carpo-lestids in the Princeton University Museum. Without their kindness, this work would not have been possible. To the late Professor Jepsen, I am particularly grateful for invitations to participate in his Princeton field expeditions in 1968, 1970, and 1971, which were largely responsible for my interest in the Carpolestidae and other Paleocene mammals.

In addition, I thank the following, who have generously loaned or permitted access to specimens under their care: Dr. M. C. McKenna, American Museum of Natural History; Dr. M. R. Dawson, Carnegie Museum; Dr. F. S. Szalay, Hunter College of the City University of New York; Dr. F. A. Jenkins, Jr., Museum of Comparative Zoology, Harvard University; Dr. A. G. Edmund, Royal Ontario Museum; Dr. J. A. Wilson, University of Texas at Austin; Dr. R. C. Fox, University of Alberta; Dr. J. A. Dorr, Jr., and the late Dr. C. W. Hibbard, University of Michigan Museum of Paleontology; Dr. R. E. Sloan and R. C. Holtzman, University of Minnesota; Drs. C. L. Gazin and R. W. Purdy, United States National Museum; Dr. P. O. McGrew, University of Wyoming; and Drs. E. L. Simons and P. D. Gingerich, Peabody Museum of Natural History, Yale University.

I have been provided with casts or illustrations of specimens, prepublication manuscripts, or other unpublished information, by T. M. Bown, Dr. P. M. Butler, Dr. W. A. Clemens, Jr., Dr. P. D. Gingerich, R. C. Holtzman, Dr. R. F. Kay, D. Krause, L. Krishtalka, M. E. Lambert, D. O'Brien, D. C. Parris, Dr. J. A. Schiebout, Dr. R. E.

Sloan, Dr. F. S. Szalay, and C. B. Wood. To all of them I am grateful.

I have profited greatly from discussions on various aspects of this study with T. M. Bown, Dr. A. W. Crompton, D. C. Fisher, J. G. Fleagle, Dr. P. D. Gingerich, Dr. G. L. Jepsen, Dr. P. O. McGrew, Dr. M. C. McKenna, D. C. Parris, Professor B. Patterson, Dr. D. E. Russell, Dr. E. L. Simons, Dr. R. E. Sloan, Dr. F. S. Szalay, and C. B. Wood.

Dr. Crompton, Mr. Fleagle, Dr. Gingerich, Dr. Jepsen, Dr. McKenna, Professor Patterson, Dr. Simons, and Dr. G. G. Simpson, have read all or part of the manuscript. Their comments and suggestions have been most useful and are much appreciated. Special thanks are due Professor Patterson for his help and encouragement during the writing of the manuscript; the text has benefited substantially from his paleontological and editorial wisdom.

Mr. A. H. Coleman prepared the photographs, which were made possible with the aid of a grant from the Society of the Sigma Xi. Figures 4 and 8 were drawn by Laszlo Meszoly. Anne Rieman assisted in typing the manuscript.

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APPENDIX

TABLE I. DIMENSIONS OF MANDIBULAR TEETH OF CARPOLESTIDS (MM).

Spec. No.	P ₄ L	P ₄ B	M ₁ L	M ₁ B	M ₂ L	M ₂ B	M ₃ L	M ₃ B	MD
<i>Elphidotarsius florencae</i> Gidley, holotype									
USNM 9411	1.7	1.3	1.3	1.2	1.3	1.3	1.8	1.1	3.1
<i>Elphidotarsius</i> sp., cf. <i>E. florencae</i> Gidley, from Rock Bench Quarry									
PU 14282	1.8	1.6	1.5	1.5	1.5	1.6	2.0	1.4	3.1
PU 14283	1.7	1.3	1.5	1.5			2.0	1.2	3.0
PU 14284	1.7	1.3	c.1.5		1.4	1.4			3.0
PU 14285	1.8	1.5	1.5	1.4	1.4	1.5	1.9	1.3	3.1
PU 14286	1.9	1.5			1.4	1.6	1.9	1.4	c.3.1
PU 14791	1.7	1.3	1.5	1.3	1.4	1.4	2.0	1.3	2.9
PU 14792	1.7	1.4	1.5	1.3	1.5	1.4	1.8	1.2	2.8
PU 14794			1.5	1.5	1.3	1.5	2.1	1.3	3.3
PU 14795					1.4	1.6	c.2.0		
PU 14796	1.9	1.5	1.5	1.4					
PU 14843			1.4	1.4	1.3	1.5	1.9	1.3	
PU 17742	c.1.9		1.5	1.5	1.3	1.4			3.4
PU 18462	1.8	1.3							
PU 18463			1.5	1.4	1.4	c.1.5			
PU 18671	1.8	1.4					1.9	1.3	c.3.0
PU 18675	1.8	1.5	1.5	1.5	1.5	1.5			3.2
PU 19801			1.6	1.6	1.6	1.7			3.3
PU 21546	1.9	1.3	1.5	1.3	1.4	1.4	1.9	1.2	3.0
PU 21547	1.9	1.5	1.5	1.5	1.4	1.5			3.5
PU 21550	1.7	1.3							
PU 21551	1.7	1.3							

TABLE I [CONTINUED]

Spec. No.	P ₄ L	P ₄ B	M ₁ L	M ₁ B	M ₂ L	M ₂ B	M ₃ L	M ₃ B	MD
<i>Elphidotarsius</i> sp., cf. <i>E. florenceae</i> Gidley, from Medicine Rocks site 1									
PU 16916		c.1.3	1.5	1.3	1.5	1.3			2.7
PU 19764	1.6	1.3	1.4	1.4	1.4	1.4			3.0
PU 19780		c.1.2	1.4	1.3					
<i>Elphidotarsius</i> <i>shotgunensis</i> Gazin									
AMNH 88311	2.0	1.2	1.4	1.1					
MCZ 18775			1.6	1.3					
<i>Carpodaptes aulacodon</i> Matthew and Granger, holotype									
AMNH 17367	2.7	1.7	1.5	1.5	1.3	1.5	1.7	1.2	3.3
<i>Carpodaptes hazelae</i> Simpson, from Scarritt Quarry									
AMNH 33853	2.6	1.7	1.6	1.4	1.3	1.5			c.3.7
AMNH 33854	2.5	1.7	1.5	1.5	1.2	1.4	1.9	1.2	3.8
AMNH 33887	2.6	1.7	1.5	1.4	1.4	1.4			3.8
AMNH 33979			1.5	1.6	1.4	1.6	1.9	1.4	
AMNH 33980	2.6	1.7	1.5	1.5	1.5	1.5	2.0	1.3	3.7
AMNH 33983			1.6	1.5	1.3	1.4			
AMNH 33984			1.4	1.4	1.3	1.5	1.8	1.2	
<i>Carpodaptes hazelae</i> Simpson, from Cedar Point Quarry									
PU 19558	2.4	1.7	1.4	1.3					
PU 19572	2.5	1.5	1.4	1.4					3.5
PU 19574	2.2	1.3	1.5	1.3	1.3	1.3	1.8	1.1	c.3.1
PU 19596	2.4	1.5	1.5	1.5					3.3
PU 19601	2.6	1.5							
PU 19936			1.5	1.4	1.3	1.5			3.4
PU 19953	2.7	1.8	1.4	1.3					
PU 19954	2.5	1.5							
PU 19955	2.5	1.8	1.5	1.2	1.2	1.3			3.3
PU 19958	2.4	1.6	1.5	1.3	1.2	1.4	1.8	1.1	
PU 19968	2.8	1.7	1.5	1.4					3.5
PU 19969	2.5	1.4							
PU 19985	2.4	1.4							
PU 20007	2.4	1.3	c.1.4	1.3					
PU 20010	2.4	1.5	1.5	1.3					
PU 20011	2.5	1.6			1.3	1.3			3.4
PU 20034			1.6	1.4					
PU 20060	2.2	1.4	1.3	1.2	1.1	1.3			3.1
PU 20064	2.4	1.4	1.3	1.3	1.2	1.3			3.5
PU 20068	2.5	1.5	1.5	1.3	1.3	1.3			3.5
PU 20084	2.6	1.6	1.5	1.4	1.3	1.4	2.0	1.3	3.6
PU 20087	2.5	1.6	1.4	1.3	1.3	1.4			3.3
PU 20610	2.5	1.6	1.5	1.4	1.4	1.4			3.5
PU 20615	2.4	1.4	1.5	1.3					3.3
PU 20630	2.3	1.4	c.1.3	c.1.2	1.2	1.2	1.7	1.0	3.2
PU 20634	2.6	1.6	1.5	1.2					
PU 20656	2.3	1.4	1.6	1.4	1.4	1.3			3.3
PU 20719	2.4	1.6	1.3	1.3	1.3	1.3	1.9	1.1	3.3
PU 20808	2.6	1.5	1.6	1.5					c.4.0
PU 20812	2.3	1.6	1.4	1.3	c.1.2	1.3			3.5
PU 20820	2.5	1.5	1.5	1.3	1.3	1.3			3.3
PU 20839	2.5	1.8	1.5	1.4	1.3	1.4	1.9	1.3	3.6

TABLE I [CONTINUED]

Spec. No.	P ₄ L	P ₄ B	M ₁ L	M ₁ B	M ₂ L	M ₂ B	M ₃ L	M ₃ B	MD
PU 20840	2.1	c.1.2							
PU 20886	2.3	1.6	1.4	1.3					
PU 20889	2.7	1.8	1.5	1.5	1.4	1.5			3.8
PU 20898	2.7	1.7	1.4	1.4					3.7
PU 20900	c.2.4		1.5	1.3	c.1.3	c.1.3			
PU 21213	2.4	1.5	1.5	1.3	1.2	1.3	1.9	1.1	3.4
PU 21266	2.3	1.5							
PU 21279	2.4	1.5	1.5	1.3	1.3	1.4			
PU 21297	2.6	1.5	1.5	1.4	1.3	1.4			3.8
PU 21299	2.5	1.6	1.4	1.3	1.3	1.3			3.4
PU 21316	2.5	1.6	1.4	1.4					3.9
PU 21317	2.4	1.5	1.5	1.3	1.3	1.4			
PU 21330	2.4	1.5	1.5	1.3	1.3	1.3			
PU 21341	2.4	1.6	1.5	1.3	1.3	1.4	2.0	1.2	3.4
PU 21350	2.4	1.5	1.4	1.2	1.3	1.3	1.8	1.2	3.3
PU 21351	2.4	1.4	1.4	1.2	1.2	1.2	1.7	1.1	
PU 21357			1.6	1.5	1.4	1.5	c.2.0	c.1.3	
PU 21384	2.7	1.5	1.4	1.3	1.3	1.4	1.9	1.2	3.8
PU 21393	2.5	1.5							
PU 21399	2.5	1.5	1.5	1.2	1.3	1.3	1.9	1.1	3.5
PU 21413	2.6	1.6	1.5	1.2	1.4	1.2	1.8	1.1	3.5
PU 21419	2.4	1.4	1.5	1.2					3.2
PU 21437	2.7	1.6							
PU 21438	2.2	1.3			1.3	1.3			
<i>Carpodaptes hobackensis</i> Dorr									
UMMP 27233	2.2	1.2	1.4	1.2	1.4	1.2			
UMMP 27234	2.3	c.1.2	1.3	1.2					
UMMP 27253	c.2.3	1.3							
UMMP 55124	2.2	1.2	1.5	1.2	1.3	1.3	1.8	1.1	
<i>Carpodaptes cygneus</i> Russell, from Swan Hills									
ROM 5622	2.2	1.2							
ROM 5623	2.0	1.2							
<i>Carpodaptes</i> sp., cf. <i>C. cygneus</i> Russell, from Cypress Hills, Alberta									
UA 5874	2.3	1.5							
UA 5875	2.1	1.4							
UA 5876	2.2	1.5							
UA 5877			1.5	1.5					
UA 5878					1.5	1.4			
UA 5879					1.4	1.4			
UA 5880							1.8	1.1	
UA 5881							1.8	1.1	
<i>Carpodaptes jepsoni</i> , new species, holotype									
PU 20716	3.2	2.2	1.9	1.7	1.7	1.7			c.5.5
<i>Carpolestes nigridentis</i> Simpson, from Bear Creek									
AMNH 22159	3.3	1.9	1.9	1.6	1.6	1.6			5.1
AMNH 22187	3.1	1.8							
AMNH 22188	3.1	2.0							
AMNH 22190	2.9	1.7	1.8	1.4	1.5	1.3			5.0
AMNH 22233	3.0	1.9	1.8	1.5	1.6	1.5	2.3	1.4	5.0
PU 20718	3.0	2.1	1.8	1.6					5.0
CM 11518			1.8	1.6					
CM 11524	3.3	1.9							

TABLE I [CONTINUED]

Spec. No.	P ₄ L	P ₄ B	M ₁ L	M ₁ B	M ₂ L	M ₂ B	M ₃ L	M ₃ B	MD
CM 11549	3.4	1.9							
CM 11557			1.8	1.4					
CM 11665	3.2	1.8							
CM 11702	3.3	1.9							
<i>Carpolestes dubius</i> Jepsen, from Princeton Quarry level									
PU 13275	3.3	2.0	1.9	1.8	1.6	1.6	2.2	1.4	
PU 13276	3.6	2.0	c.1.9	c.1.7	c.1.5	c.1.6			
PU 14235			1.9	1.8	1.5	1.6			
PU 14341			2.0	1.7	1.6	1.5			
PU 14342	3.4	2.1	1.9	1.6					
PU 14344	3.0	2.1	1.8	1.6	1.6	1.6			4.6
PU 14345	3.2	2.0	1.7	1.5					
PU 14346	3.3	1.8	1.9	1.5	1.5	1.4			
PU 17646			1.8	1.5	1.4	1.5	2.3	1.4	4.0
PU 17647			1.6	1.6	1.5	1.5			
PU 17710	c.3.2	c.1.9	1.8	1.5	1.5	1.5	2.0	1.3	4.9
PU 17856			1.8	1.5					
PU 17857	3.3	2.0							
PU 17858	c.3.6	c.2.2	2.0	2.1					
PU 17860	3.6	2.0							
PU 17861	3.5	2.1	1.9	1.8					c.5.0
PU 17926	3.1	2.1	2.0	1.7	1.7	1.7			4.8
PU 19013	3.1	1.8							
PU 19018			1.9	1.6	1.6	1.6			
PU 19023	3.3	2.1							
PU 19030	3.3	1.9	2.0	1.7					
PU 19031	3.2	2.3	1.9	1.6	1.5	1.6			
PU 19064		c.2.1	1.9	1.9					
PU 19095	3.6	2.0							
PU 19109	3.3	2.0							
PU 19385	3.4	2.1	1.9	1.7	1.6	1.6	2.2	1.4	5.3
PU 19406	3.0	2.0	1.7	1.6	1.5	1.5	2.0	1.4	
PU 19409	3.5	2.2	2.0	1.8	1.5	1.6	2.1	1.4	5.5
PU 19849	3.5	2.2							
PU 19886	3.3	1.9	1.9	1.6					
PU 21548	3.3	1.9							
PU 21549	3.3	1.9							
<i>Carpolestes</i> sp., from various localities									
PU 13284	3.0	1.7							
PU 14853	3.5	2.2	1.7	1.5					
PU 18102	3.1	c.1.7							
PU 18315	3.8	2.5	2.0	1.8					
PU 20720			1.8	1.5					
PU 20721	3.2	1.8	1.9	1.5					
PU 21227a	3.1	1.6							
PU 21227b	3.2	2.0	1.9	1.6					
PU 21227c	3.1	2.1	1.8	1.6					
AMNH 88198	3.3	1.9	1.8	1.5	1.5	1.4			5.0
USNM 21280	2.7	1.7							

TABLE II. DIMENSIONS OF MAXILLARY TEETH OF CARPOLESTIDS (MM).

Spec. No.	P ³ L	P ³ B	P ⁴ L	P ⁴ B	M ¹ L	M ¹ B	M ² L	M ² B	M ³ L	M ³ B
<i>Elphidotarsius</i> sp., cf. <i>E. florencae</i> Gidley, from Rock Bench Quarry										
PU 17439	1.3	1.6	1.6	2.1	1.4	2.2	1.3	2.2	1.2	2.0
PU 17736			1.5	1.9	1.3	2.1				
<i>Carpodaptes hazelae</i> Simpson, from Scarritt Quarry										
AMNH 33855	2.0	2.2	1.8	2.3						
AMNH 33980	2.0	2.3	2.0	2.6	1.4	2.3	1.4	2.2	1.3	2.0
AMNH 33981	1.9	2.1	1.8	2.3						
AMNH 33982	1.8	2.0	1.5	2.1	1.3	2.1				
AMNH 33985	1.9	2.1								
<i>Carpodaptes hazelae</i> Simpson, from Cedar Point Quarry										
PU 19939	1.9	2.0	1.7	2.2	1.3	1.8	1.2	1.8	1.2	1.6
PU 20065	1.8	2.0	1.7	2.2						
<i>Carpodaptes cygneus</i> Russell, from Swan Hills										
ROM 05624	1.6	1.6								
<i>Carpodaptes</i> sp., cf. <i>C. cygneus</i> Russell, from Cypress Hills, Alberta										
UA 5857	1.7	1.8								
UA 5858	1.8	1.8								
UA 5861			1.7	2.1						
UA 5862 [M ² ?]							1.3	2.0		
UA 5872									1.1	1.7
<i>Carpodaptes</i> sp., from Princeton Locality 11 in the Crazy Mountain Field										
PU 14639			1.7	2.4	1.4	2.1	1.3	2.0		
<i>Carpoleptes nigridens</i> Simpson, from various localities										
AMNH 22196	3.2	2.4								
PU 17978	3.1	2.3								
PU 19543	2.8	2.3								
YPM 24614	3.3	2.5								
<i>Carpolestes dubius</i> Jepsen, from Princeton Quarry Level										
PU 13305	2.5	2.5	2.2	2.2	1.6	2.1	1.5	2.1		
PU 14069	2.4	2.2	2.1	2.2	1.6	2.2				
PU 14077	2.4	2.3	2.2	2.0	1.5	2.2	1.5	2.0	1.3	1.9
PU 14343	2.5	2.5	2.3	c.2.5						
PU 14347	2.6	2.5								
PU 17707	2.4	2.3	2.1	2.1						
PU 17708							1.5	2.3	1.4	2.2
PU 17709 r	2.5	2.3	2.2	2.2	1.5	2.4	1.5	2.3	1.3	2.0
PU 17709 l	2.4	2.3	2.2	2.2	1.5	2.5	1.5	2.3	1.3	2.0
PU 17859	2.4	2.4	2.2	2.1						
PU 17927	2.6	2.3	2.2	2.2	1.6	2.1				
PU 17963			2.0	1.9	1.5	2.1	1.4	2.0		
PU 19081	2.5	2.4								
PU 19349	2.5	2.7	2.3	2.3	1.8	2.4	1.5	2.3	1.3	2.0
PU 19422 r	2.7	2.5	2.3	2.2						
PU 19422 l	2.7	2.5			1.6	2.4	1.5	2.2	c.1.3	2.0
PU 19436			2.4	2.1						